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Reproductive Ecology Of Five Arctic Species Of Pedicularis (scrophulariaceae)

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REPRODUCTIVE ECOLOGY OF FIVE ARCTIC SPECIES OF PEDICULARIS (SCROPHULARIACEAE)

by

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ABSTRACT

A field study of seed production in five species of Pedicularis, four of which reproduced only by seeds, revealed considerable variability among species in characteristics associated with reproduction by seeds and in the success of seed production at an arctic location (McConnell River, Northwest Territories, Canada, 60°50'N, 94°25'W). Observations during four years (1965-1968) indicated that most plants of all species were perennial but plants of two species (Pedicularis labradorica Wirsing, P. parviflora Sm.) generally attempted seed production only once. These latter species represent a type of life history (monocarpic perennial) which has seldom been recognized in arctic plants.

Conditions at the McConnell River were adequate for seed production in each species in each year studied with the possible exception of two species (P. parviflora, P. sudetica Willd.) in 1968. Analyses of seed output data showed that there was greater variability in seed production among randomly selected sites within a year than among years.

The overall mean number of seeds per fruiting attempt (per plant) ranged among species from 8 to 164 and it represented between 2% and 40% of the estimated potential seed output per species (defined as reproductive efficiency).

The species with the lowest (P. sudetica) and highest (P. parviflora) reproductive efficiencies had the highest (28%) and lowest (16%) percentages of reproductive failures (fruiting attempts with no seeds), respectively.

One unexpected condition which contributed to reproductive failure and to some of the differences in seed production between sites and species was seed and capsule predation, found in a total of 26% (Pedicularis lapponica L.) to 61% (P. sudetica) of all the completed fruiting attempts. The species with the lowest reproductive efficiency had the highest frequency of predated reproductive attempts, although predated plants in all species did not necessarily have fewer seeds than nonpredated plants.

A second condition contributing to reproductive failure and low reproductive efficiency in some species of Pedicularis appeared to be associated with inadequate or inappropriate pollination. Only one species (P. flammea L.) consistently showed no significant difference in the frequency of control and bagged inflorescences with seeds. Additional results of insect exclusion experiments suggested that seed production could be partially dependent on pollen vectors in three species (P. labradorica, P. parviflora, P. sudetica) and totally dependent on pollen vectors in one species (P. lapponica). Four species of insects, which together were observed visiting flowers of only three species of Pedicularis in 1968, have been identified as potential pollinators.

Although it is generally held that conditions adversely affecting seed production in the arctic are physical factors (i.e. short summers, low temperatures), the two conditions identified here indicate that biotic factors can have important effects on the success of seed production in some arctic plants.

ACKNOWLEDGEMENTS

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Special appreciation is given to my husband, Charles,

who made it possible for me to be at the McConnell River in 1964, and to obtain the background experience which aided me in gaining support for this project. I also thank Margaret Chandler for her able assistance with the field research in 1967.

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Chapter 1

INTRODUCTION

In the arctic, conditions favoring seed production do not exist for some species; for other species, the right combination of favorable conditions may not occur every year (Bliss 1962, Billings and Mooney 1968, Beschel 1970). Some plants may not complete flowering or fruiting, some may produce abundant fruit but no seeds and others may produce seeds which fail to germinate (Resvoll 1917, M. Porsild 1920, Mathiesen 1921, Holttum 1922, Sørensen 1941, A. Porsild 1951a, Bliss 1958, 1962, Billings and Mooney 1968 and others). The cumulative effect of adverse conditions on reproduction by seeds in arctic plants is evident in the low frequency of annual, or single-reproducing, life histories, the replacement of sexual reproduction by agamospermy and the widespread occurrence of various forms of vegetative propagation (Porsild 1951a, Billings and Mooney 1968).

The conditions commonly cited as contributing to poor seed production are low temperatures, exceptionally short growing seasons and late development of plants in areas of snow accumulation (e.g. Bliss 1962, Billings and Mooney 1968, Beschel 1970). Nevertheless, species of plants which reproduce, or attempt to reproduce, by seeds in the arctic have received little study to determine when or how often

these or other conditions are responsible for failures in seed production. Furthermore, without quantitative documentation of seed output in arctic plants, it is impossible to evaluate the levels of seed production for any particular year, or the reproductive capacity of a species.

Recent interest in seed production in arctic and subarctic plants has arisen in response to questions of (1) the natural recolonization of disturbed areas in the tundra and (2) the possibility of developing native northern plants (e.g. grasses, sedges, and legumes) for forage crops (Klebesadel 1971). At the initiation of a current study of legumes in Alaska, Klebesadel (1971) noted that virtually no data were available to indicate the seed yields which might be expected from any of the native legumes.

This thesis project was planned to compare the relative success in seed production among species within one genus in an arctic area and to determine whether the different species within that genus shared the same problems, if any, associated with seed production. In addition to obtaining information on the quantities of seeds produced and the factors affecting the relative success of seed production, this approach should provide clues to the following basic question: Has the presumed severity of arctic conditions resulted in the selection of one particular "seed-reproducing phenotype" or strategy (Harper 1967) among the congeneric

species occurring in the same area? The research was initiated by first selecting a location for the study and then choosing the plants from among those available in the study area.

The primary study area was located at the mouth of the McConnell River (Northwest Territories, Canada, 60°50'N, 94°25'W), on the west coast of Hudson Bay (Figure 1.1). This area was chosen for the following practical reasons: (1) I had previously worked in the area and was familiar with the flora, (2) the area could be reached relatively economically from Churchill, Manitoba, and (3) the area was included within a "protected" Federal Migratory Bird Sanctuary (McConnell River Bird Sanctuary). Additional field studies were conducted near Churchill, Manitoba.

Although latitudinally the McConnell River is south of extensive subarctic areas (sensu Löve 1970) in North America, the cool climate, frozen ground conditions, poorly developed soils, and specialized flora and fauna would be considered characteristic of a terrestrial arctic ecosystem (Porsild 1951a, Polunin 1951, Brown 1960, Downes 1964, 1965, Bryson 1966, Britton 1966, Bird 1967, Thompson 1968, Löve 1970). Some authors would further designate the area biogeographically as "low arctic" (Porsild 1951a, Polunin 1951, Downes 1964, 1965). The area around Churchill, Manitoba, is generally designated as subarctic (Löve 1970) or forest-tundra ecotone. These two areas are described briefly in Appendix B. The field study areas will henceforth

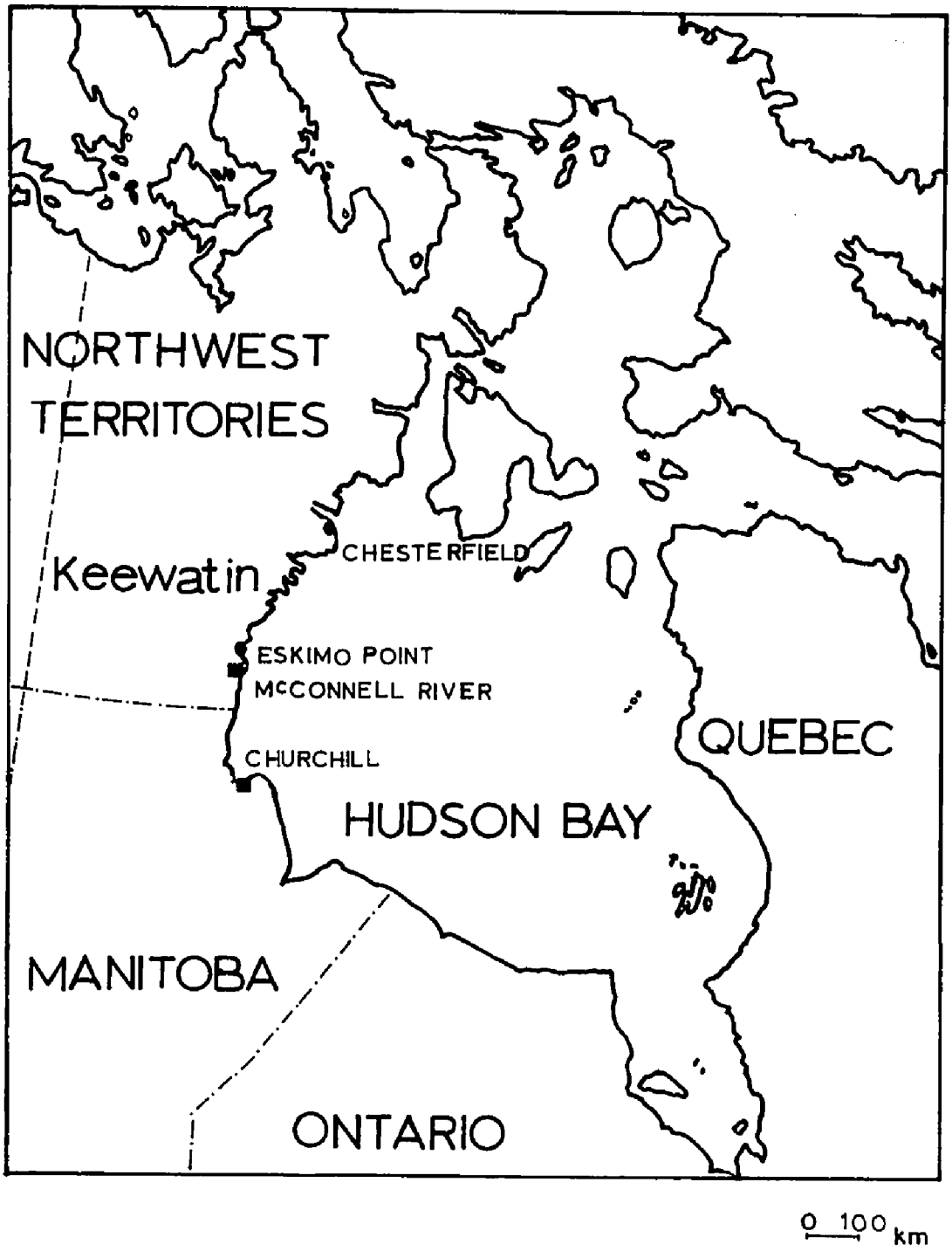

Figure 1.1. Locations of field study areas (■) and adjacent communities in central Canada.

be referred to as the McConnell River and Churchill.

The following criteria were used to select the taxa to be studied. The genus selected should be represented by at least five species which reproduced by seeds. The number five was set arbitrarily: a study of five species should expose more of the factors influencing seed production than a study of only one or two species. In addition, the plants of each species should be rapidly identifiable at different stages of development, definable as individual plants, and sufficiently abundant for sampling.

Of the approximately 150 species of vascular plants that I collected at the McConnell River in 1964 and which might, therefore, have provided the experimental material, five genera were represented by five or more species: Carex (ca. 23), Salix (ca. 9), Ranunculus (5), Saxifraga (5) and Pedicularis (5). Carex and Salix were eliminated from consideration here because of the problems of identification and the delimitation of individuals; Ranunculus, because of the problem of delimiting individuals in the two species which spread by runners; and Saxifraga, because two of the five species reproduced by bulbils or bulblets.

Therefore, the fifth genus (Pedicularis), represented by five species which reproduced by seeds, was chosen for study, even though plants of one species were rhizomatous and hence difficult to delimit. A "plant" of the rhizomatous species was arbitrarily defined for sampling as one node of

a rhizome, identified by the presence of a vegetative rosette or a floral shoot.

The genus Pedicularis (Scrophulariaceae, subfamily Rhinanthoideae) contains several hundred species (600 to 800, Li 1951) of herbaceous plants which occur primarily in alpine and arctic areas of the northern hemisphere. Some of the species of Pedicularis are commonly known as lousewort, fernleaf, fernweed, or betony.

Twenty-one species of Pedicularis are known to reach the circumpolar arctic (Polunin 1959); thus, approximately one-quarter of the arctic species of Pedicularis are available for study at the McConnell River. The five species at the McConnell River are Pedicularis flammea L., P. labradorica Wirsing, P. lapponica L., P. parviflora Sm. and P. sudetica Willd.

Observations on reproduction from other locations suggest that the species of Pedicularis which occur at the McConnell River are particularily interesting for a comparative study of seed production because they include species reported to fruit either well, or, poorly. For example, in Greenland, Pedicularis flammea and P. labradorica appear to fruit abundantly whenever observed whereas P. lapponica fruits very poorly and possesses many empty capsules, or capsules with few seeds (Porsild 1920, Mathiesen 1921). According to Porsild, Pedicularis lapponica is "the poorest fruit-setting species in Greenland" (in Mathiesen 1921). Poor seed production in Pedicularis lapponica

has also been observed in Novaya Zemlya (Ekstam in Mathiesen 1921).

Another question of considerable interest in the study of seed production in arctic species of Pedicularis concerns the apparent adaptation of the flower to bumblebee pollination (Aurivillius 1883, Müller 1884, Kerner 1894-1895, Sprague 1960, 1962b, Macior 1968a, 1968b, and others) and the rarity of observations of visits by bumblebees in some arctic areas (Mathiesen 1921, Mosquin and Martin 1967). Despite the relatively specialized flower type, some species of Pedicularis are known to produce seeds in northern areas where bumblebees apparently are relatively rare (Ekstam in Mathiesen 1921, Lagerberg et al. 1957, Savile 1959) or where bumblebees are not known to exist (e.g. Spitzbergen, Aurivillius 1883).

Some of the paradoxical information relating to seed production in species of Pedicularis can be illustrated by Pedicularis labradorica. Porsild (1920) and Mathiesen (1921) reported that plants of P. labradorica in Greenland produced abundant seeds. The indirect evidence available from Greenland suggests that seeds of Pedicularis labradorica are produced by sexual reproduction (Jørgensen, Sørensen and Westergaard 1958, see also Appendix C). According to Mathiesen (1921) self-pollination could occur "only with difficulty" in Pedicularis labradorica in Greenland because the anthers were separated from the stigma in the flower. However, there apparently are no records of insects visiting

the flowers and, therefore, no known means of cross-pollination. Assuming that reproduction is sexual, and that pollination is necessary for seed production in P. labradorica, one or more of the following circumstances might account for the paradox: (1) the seed production was overestimated, (2) the plants self-pollinated more readily than postulated from floral structure, or (3) pollinators were present but simply not observed.

The criterion used in this study to evaluate the relative success of seed production in each species of Pedicularis at the McConnell River was the proportion of ovules which became seeds. This was determined by comparing estimates of the actual seed production per flowering-fruiting attempt to estimates of the potential seed production per flowering-fruiting attempt. This relationship, an expression of actual seed production as a percentage of the potential seed production (per flowering-fruiting attempt) was termed "reproductive efficiency" (sensu Smith 1954, Lyons 1956). It provided a measure of the efficiency, or success, of seed production which could be compared among species regardless of the number of times that plants of different species reproduced. The "most successful species", in this case, was defined as the one with the highest reproductive efficiency.

The actual seed production, also termed "seed output" (Salisbury 1942), was measured just before seeds would normally be released from a plant and refers to the number

of seeds produced on a plant in a single flowering-fruiting attempt. (A flowering-fruiting attempt will subsequently be designated as a "reproductive attempt".) The estimated average seed production for a species of Pedicularis at the McConnell River was based on data obtained from reproductive attempts sampled during three or four years. Potential seed production was determined from estimates of the average number of ovules per ovary and the average number of ovaries per plant (one ovary per flower).

The concept of "success" or "failure" was also applied to an individual reproductive attempt. For example, if a plant did not bear any seeds during its reproductive attempt, the attempt was termed a reproductive failure. If it produced at least one seed, the attempt was arbitrarily termed a reproductive success. The concept of success or failure, as applied here to a reproductive attempt, refers to the bearing of seeds only. It does not include the possibility that a plant may contribute genetically, through cross-pollination, to the production of seeds on another plant.

The main parts of this thesis involve estimating potential and actual seed production and comparing them to determine the reproductive efficiency of each species (Chapters 5 and 6). The frequencies of reproductive failures and some of the factors contributing to them are examined in Chapters 7 and 8. Chapters 2 and 3 introduce methods and analyses, and the plants, respectively. Chapter 4 is

an introduction to reproduction in the five species of Pedicularis, primarily at the McConnell River.

Chapter 2

METHODS AND ANALYSES

2.1 Introduction

The research for this thesis consisted primarily of observations and experiments conducted in the field, supplemented by the examination of collected specimens. It also included preliminary tests of seed germination conducted at the University of Western Ontario.

Table 2.1-1 shows the schedule of field work at the McConnell River and at Churchill. Access to the McConnell River from the settlement of Eskimo Point, N.W.T., was logistically and financially possible in May when snow was present, or any time after late June or early July, when the Hudson Bay coast was free of ice. The latter arrival time was chosen primarily because it was possible to test field techniques and make observations on four species of Pedicularis in Churchill before arrival at the McConnell River. Field work was terminated at the McConnell River about 21 August each year when transportation could be coordinated with other workers leaving the area.

The term population, as used in this study, refers to the individuals of a species which occur within a geographic area or location, such as the study area at the mouth of the McConnell River or near Churchill (i.e. topodeme, Gilmour and Gregor 1939).

Table 2.1-1. Schedule of field work.

YEAR	LOCATION	DATES
1965	McConnell River	10 July - 20 August
1966	Churchill	11 June - 30 June
	McConnell River	6 July - 21 August
	Churchill	23 August - 5 September
1967	Churchill	15 June - 27 June
	McConnell River	27 June - 20 August
	Churchill	21 August - 25 August
1968	McConnell River	7 July - 21 August

Methods and analyses which are referred to in more than one chapter are given in the following sections of this chapter. Additional details on methods are presented later with the appropriate parts of the thesis. For brevity, when reference is made to more than one of the species of Pedicularis involved in this study, the citation will generally read simply "in Pedicularis" rather than "in five species of Pedicularis" or "in Pedicularis spp.".

The Appendices of the thesis are indicated by letters: thus, the tables and figures in them will include a letter to indicate the appendix where they are found (i.e. Table B-1).

2.2 Sampling procedures

Sampling of plants, unless otherwise indicated, was conducted within the square kilometers of the study area numbered 13, 23, 14, and 24 (Figure B-1) according to the following general procedure. This area, using the permanent

grid as a basis, was subdivided (on paper) into 100 m by 100 m blocks and one corner of each block was assigned a number. Sampling involved drawing a random number to indicate a corner of a block (used as a starting point) and then drawing a pair of random numbers (from 0 to 100) to indicate the position of the sampling point (i.e. the number of steps) within the block. The nearest plant of the appropriate species of Pedicularis to the point (within an arbitrary maximum limit of 50 steps) was sampled. To avoid inclusion of the same plant more than once, a point within 5 m of a formerly sampled position was omitted.

The main exception to this general sampling procedure involved the grouping of samples of plants into areas called "sites" for the reproductive survey. A central point for a site was located in the manner described in the previous paragraph for a sampling point except that only blocks adjacent to the permanent grid line 04-14 were used. Starting at the chosen point, all plants of one or more species of Pedicularis which could be found around the point were temporarily marked and numbered. A separation of at least 30 cm, or open water, was allowed between marked nodes of Pedicularis lapponica to reduce the possibility of using the same plant twice.

The area inspected around the central point was gradually increased until twice as many plants were numbered as would be used in the final study. The maximum size of a site was arbitrarily set (a radius of 11 m or less, or, an

area of approximately 400 m^2 or less); if sufficient plants could not be found, a new point was drawn. Thus, a site was a randomly chosen "local area" occupied by a group of sampled plants. Conditions such as elevation, soils, moisture and plant species composition were usually heterogeneous within a site.

The actual plants for sampling were randomly chosen from the temporarily marked plants in the site. It was anticipated that this procedure might overcome some of the bias of finding the larger plants of each species first. Subsequent experience indicated that plants less than at least three years old were unlikely to have been detected by this sampling because of their minute size. Therefore, the marked plants represent a biased sample of the total plant population (excluding seeds) within each local area. One compensation of this bias was that greater numbers of plants of reproductive age were marked.

2.3 The reproductive survey of marked plants

A technique of marking the individual plants to be sampled was used in this survey of seed production primarily to base the estimates of average seed production, and of reproductive efficiency, on the number of individual plants which attempted flowering and fruiting. This contrasts with the general practice of estimating the seed output of plants from collections of fruiting plants (i.e. plants which possess fruit(s) and seed(s), cf. Salisbury 1942). Unless all the plants which flower also produce fruits and seeds,

a condition which may be uncommon in arctic plants, counting seeds only from the plants with fruits could lead to considerable overestimation of the seed production and reproductive efficiency of a plant population. Marked plants also made it possible to observe the development of flowers and fruits throughout a single growing season and to observe the development of plants over several growing seasons.

The sampling scheme for the reproductive survey was designed to permit quantification of seed production per reproductive attempt at three levels: (1) among plants within sites, (2) among sites within years, and (3) among years. The basic procedure for selecting sites and plants was presented in Section 2.2.

Ten plants per species, per site (two or three sites per species), were marked in 1965 by using wooden garden labels 10 inches (25.4 cm) long placed about 5 cm from each plant. Most of these labels were destroyed by moving ice (June 1966) or disturbed by animals. Consequently, new plants (20 per species, per site) had to be marked in 1966. These plants were indicated by markers made from 30 cm lengths of number nine brace wire and coded with aluminum tags. The number of sites sampled was increased from 5 in 1965 to 11 in 1966, increasing the number of marked individuals to 100 per species; a site contained marked plants of one to four species of Pedicularis. The sites are described briefly in Table A2.3-1. Twenty additional plants of Pedicularis parviflora were marked in

Sites 7, 9, and 10 in 1967.

In a less extensive reproductive survey initiated at Churchill, Manitoba, in June 1966, five sites were randomly chosen using roads parallel to the shoreline of Hudson Bay as the base line for sampling. The methods of locating the sites and the plants were similar to those described for the McConnell River. Twenty-five plants were given permanent markers in each site (three or four sites per species). The sites are described in Table A2.3-2.

At the McConnell River, observations were continued on the marked plants or their remains in 1966, 1967 and 1968, except where markers were missing. The information recorded included the condition or development of the plant during that growing season (i.e. vegetative rosette only; attempting flowering and fruiting, dead) and parameters of capsule and seed production. Because of the slow rate of decay, it was also possible to note the presence of inflorescences from one or two previous reproductive attempts.

Figure 2.3-1 summarizes how the success or failure of a reproductive attempt was scored, and how three categories of plants, or reproductive attempts, were distinguished on the basis of the condition of the reproductive attempt observed in the field. For example, if a reproductive attempt lacked capsule(s), or had capsule(s) but lacked seed(s), and showed no evidence of damage to the ovaries, ovules or capsules, the plant was scored as an "incomplete reproducer".

The number of seeds on plants of Pedicularis at the

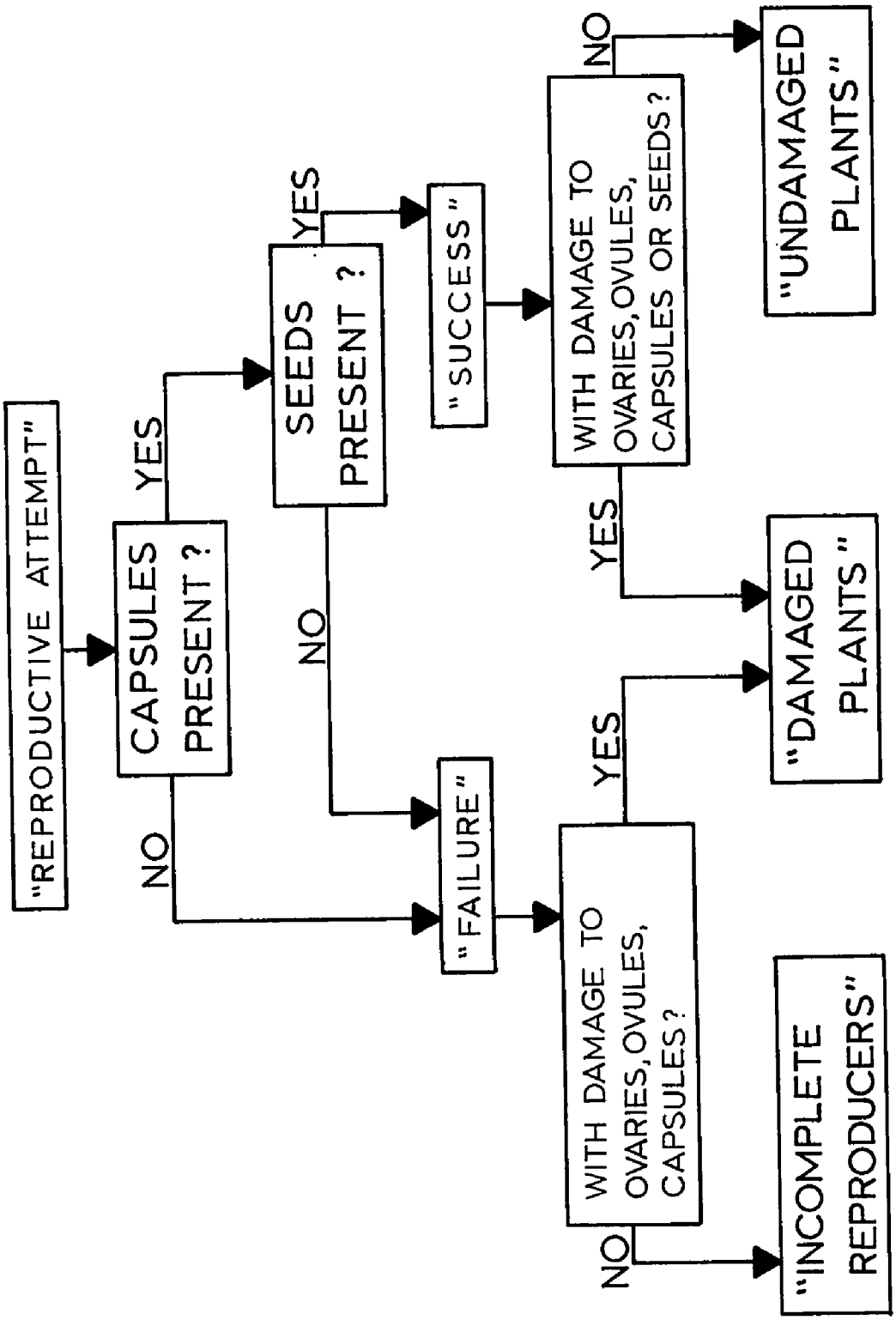

Figure 2.3-1. Evaluation of "reproductive attempts".

McConnell River was counted from capsules which were cut from the stem(s) of a plant within three days of finding the earliest dehisced capsules of the appropriate species anywhere within the study area (for dates of first capsule dehiscence, see Table 4.3-2). This procedure was used to judge when fruits of a species were approaching maturity: it allowed the capsules of the marked plants to be collected before they had dehisced and released seeds.

Since senescence of the stems and reproductive parts of Pedicularis flammea, P. labradorica, P. lapponica and P. sudetica also appeared to be well underway at the time of first capsule dehiscence, as judged by the colors (red, yellow, brown) of these parts and the number of seeds detached from the placenta inside the capsules, I have assumed that capsule (and calyx) removal did not have a significant effect on the subsequent development and seed production of these species. Although stems of Pedicularis parviflora were still green at the time of capsule harvest, plants of this species reproduced only once.

In 1968, there was no evidence of capsule dehiscence in any plants of Pedicularis parviflora and P. sudetica when field work was terminated at the McConnell River on 21 August. Consequently, the capsules of the marked plants of these species were not harvested in 1968. There were no reproductive plants of P. labradorica remaining in the survey in 1968.

The seeds of the species of Pedicularis studied are basically elongate to oval ("cigar-shaped", P. flammea,

P. labradorica, P. lapponica and P. sudetica) or ovate (P. parviflora) and vary in size (largest seeds, approximately 3 mm long and 2 mm in diameter), depending on the species. Seeds of three of the species are illustrated in Lange (1870-1871). Seeds, as defined here for counting, included the normal-appearing seeds found detached from the placenta (inside the capsule) and the large plump ovules, similar in size to a normal seed but lacking the typical grayish or brownish coloration and still attached to the placenta. These ovules were readily distinguished from the minute, withered ovules within a capsule.

All seeds, as just defined, are tentatively assumed to be of equally good quality (i.e. all seeds of all species are assumed to be viable). The results of preliminary attempts to assess seed quality are considered in Chapter 6 and Appendix F.

At Churchill, the seeds remaining in capsules which had already dehisced were counted in 1966. Since seeds were released before I could return to Churchill from the McConnell River, no information is available on the quantity of seeds actually produced.

2.4 Statistical analysis

Table 2.4-1 summarizes the procedures used here for the analyses of data. The primary references consulted were Steel and Torrie (1960), Snedecor and Cochran (1967) and Sokal and Rohlf (1969). The actual analyses were

Table 2.4-1 Procedures for analyses of data.

PROCEDURES FOR ANALYSES
2 X 2 tests of independence
by chi-square test (SR[1]: 589)
by exact test (when largest sample size is less than 50) (Finney et al. 1963, Bennett and Horst 1966)
Data examination
shape of frequency distribution: skewness (SR: 116-118, 171-172)
transformation of variables: square root, logarithm (SR: 380-385)
Dispersion
coefficient of variation (SR: 62-63)
estimation of variance components (SR: 210-213)
equality of two variances: F-test (SR: 186)
homogeneity of several variances: Bartlett's test (SR: 370-371)
Location
equality of means
with homogeneous variances: t-test, one-way analysis of variance (SR: 220-221, 206-219)
with heterogeneous variances: approximate t-test (SR: 375)
a posteriori multiple comparison of means: the Student-Newman-Keuls test (SNK test) (SR: 239-245)
two-level nested analysis of variance (SR: 256-269, 274-280)
nonparametric comparisons:
Kruskal-Wallis test: (SR: 388-390)
STP (simultaneous test procedure): (SR: 396-397)
Mann-Whitney U-test (SR: 392-394)

1. SR = Sokal and Rohlf 1969, followed by pages of reference.

conducted, unless otherwise noted, according to the methods described in Sokal and Rohlf (1969) and details of analyses are available in their book as indicated in Table 2.4-1.

The following notations are used, primarily in tables, throughout the thesis: df = degrees of freedom, t = t value, t' = approximate t value, F = variance ratio, χ^2 = chi-square value, log = logarithm, ns = not significant ($P>0.05$), * = significance at $P<0.05$, ** = significance at $P<0.01$, and *** = significance at $P<0.001$.

Three general circumstances influenced the kinds of data collected and their analyses. First, this was a preliminary study and no prior quantitative knowledge of the characters was available. Thus, a primary concern was to identify some of the sources and amounts of variability (e.g. within plants, among plants, among sites, among locations or among years). Second, sample sizes were variable and frequently small. This was due to the necessary division of sampling and examination time among five species and to other factors such as plant disturbance, predation, unknown frequency of reproductive attempts, and unknown mortality levels of plants. Third, comparisons, especially between species, frequently introduced relatively high levels of heterogeneity which had to be considered in relation to the assumptions required for a particular analysis (e.g. homogeneity of variance for analysis of variance). The consequences of these circumstances are important: (1) estimates of variation were not available

for refinement of sampling technique or determination of appropriate sample sizes and (2) it was not possible to detect small differences between sample means where there were large amounts of variability or relatively small sample sizes, or both.

If an F-test or Bartlett's test of homogeneity of variance indicated that the assumption of homogeneity of variance for a t-test or an analysis of variance could not be met, variables were transformed to see if the new values met the required assumption. Two transformations, a common logarithmic transformation and a square root transformation, were used in this study. If tests of variance using transformed values indicated homogeneity of variances, further analyses were conducted using those values. According to Sokal and Rohlf (1969) a transformed scale which makes the sample variances homogeneous, may also correct other departures from the assumptions required for the analysis of variance. If tests of variance using the transformed values indicated significant heterogeneity of variances, the original data were then used in tests which did not assume that variances were homogeneous, such as an approximate t'-test, the Kruskal-Wallis test, the Mann-Whitney U-test, and nonparametric multiple comparisons by STP (see Table 2.4-1 for specific references).

In testsof independence, where some comparisons were quite obviously different (e.g. all plants of one sample and no plants of another sample were damaged) the tests

were made directly in two-way (2 X 2) tables instead of first examining multiway tables. The tests of independence were of the Model I type (Sokal and Rohlf 1969) where only the total sample size was fixed; for example, the number of plants examined in a site was fixed but the numbers of these which flowered or which were predated by insects were not controlled. If the larger of two samples to be compared was less than 50, exact probability tests (two-tailed) were made using tables compiled by Finney et al. (1963) and by Bennett and Horst (1966). With larger samples, independence was tested by the chi-square technique.

Chapter 3

AN INTRODUCTION TO THE SPECIES AND POPULATIONS

3.1 Taxonomy and geographic distribution

The five species of Pedicularis which occur at the McConnell River are P. flammea L., P. labradorica Wirsing (syn. P. euphrasioides Stephen), P. lapponica L., P. parviflora Sm., and P. sudetica Willd., according to the nomenclature given them by Scoggan (1957) and Porsild (1964) which has been followed in this study. Voucher specimens of all five species are located in the following herbaria: University of Western Ontario (UWO), Canada Department of Agriculture (DAO), and National Museum of Canada (CAN). In addition, specimens of one species, Pedicularis parviflora Sm., were submitted to Dr. E. Hultén at the Naturhistoriska Riksmuseet, Stockholm.

The northern North American distributions of the species studied are shown in Figure 3.1-1 on maps which were redrawn from world distribution maps given by Hultén (1968) with one major modification: Pedicularis macrodonta Richards., as given in Hultén (1968), is included here within P. parviflora Sm. (see Scoggan 1957). From the maps it can be seen that Pedicularis sudetica is the only one of these species which occurs on the most northerly islands of the Canadian Arctic Archipelago and P. parviflora is the only one which does not occur on any islands of the

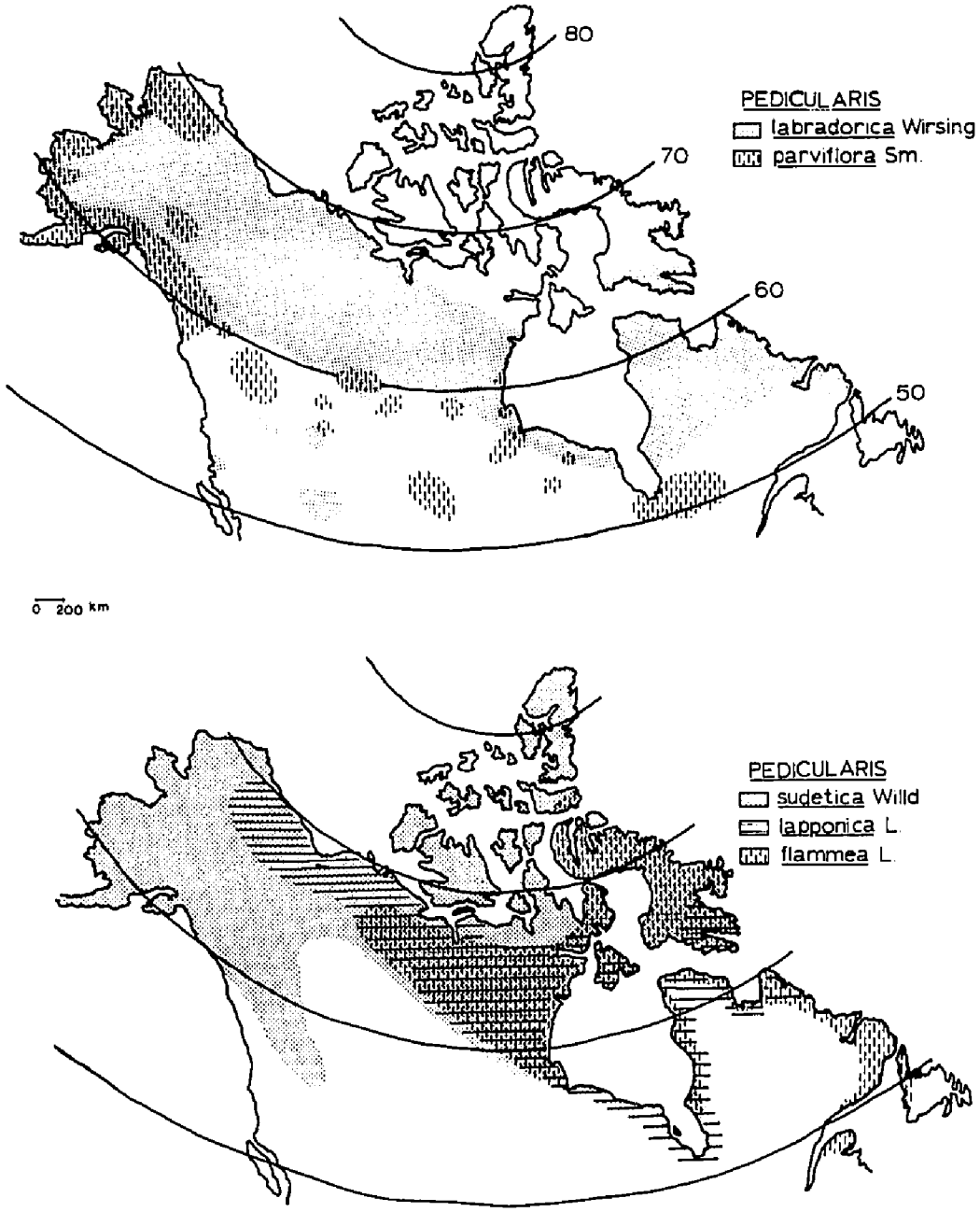

Figure 3.1-1. Northern North American distribution of five species of Pedicularis (from Hultén 1968)

Archipelago. The plants of Pedicularis parviflora found at Churchill and at the McConnell River both represented new records for the areas and a northward extension of the known range of the species along Hudson Bay (Cody and Porsild 1968). Dot maps showing more specific locations of plants of these species in North America may be found in Raup (1947), Porsild (1964) and Hultén (1968). Pedicularis sudetica is the only one of these five species known to occur south of the area shown by the maps in Figure 3.1-1: it also occurs in the Rocky Mountains in Colorado (Hultén 1961, 1964, 1968).

3.2 Microdistribution of Pedicularis at the McConnell River

The elevation of plants, relative to the level of open water, was recorded in two randomly selected sites to illustrate approximately where plants of the five species of Pedicularis occur within the McConnell River study area. The sites were chosen as described in Section 2.2 except that at least four species of Pedicularis were required around a point and that all nodes of Pedicularis lapponica were marked.

A reading of elevation for each plant was taken at the base of the stem (ground level) and a reading of water level was taken at the surface of open water present within each site, using a transit and stadia rod. All readings in a site were taken on a single day (Site 1, 23 July; Site 2, 22 July; 1967) since the water level varied depending

on the amounts of melted water, rainfall, or drainage. The elevation at water level was assigned as zero and all other readings were expressed relative to it.

The positions of plants in these two sites showed (1) a partial and variable separation of species by elevation depending on the site and the species and (2) the occurrence of species at variable levels above open water in different sites (Figure 3.2-1). For example, Pedicularis labradorica occurred between 50 and 120 cm above open water in Site 1 and between 5 and 35 cm above open water in Site 2. One possible explanation for this difference is that the coarser textured parent materials under P. labradorica in Site 2 provided drainage and other associated conditions similar to those at higher elevations in Site 1. The reasons for the absence of Pedicularis flammea in Site 2 are not clear. No study has been made of the factors which affect the microdistribution of these species at the McConnell River.

Within each of these sites, the density of individual plants of Pedicularis was relatively low; although, estimated subjectively, these sites appeared to have relatively dense populations of Pedicularis compared to other parts of the study area. Table 3.2-1 illustrates the number of individual plants of four species (excluding P. lapponica because individual plants are not readily delimited) in randomly thrown quadrats (50 x 100 cm) in Site 1. These values represent a maximum density of individuals since plants were counted only in those quadrats which had an individual

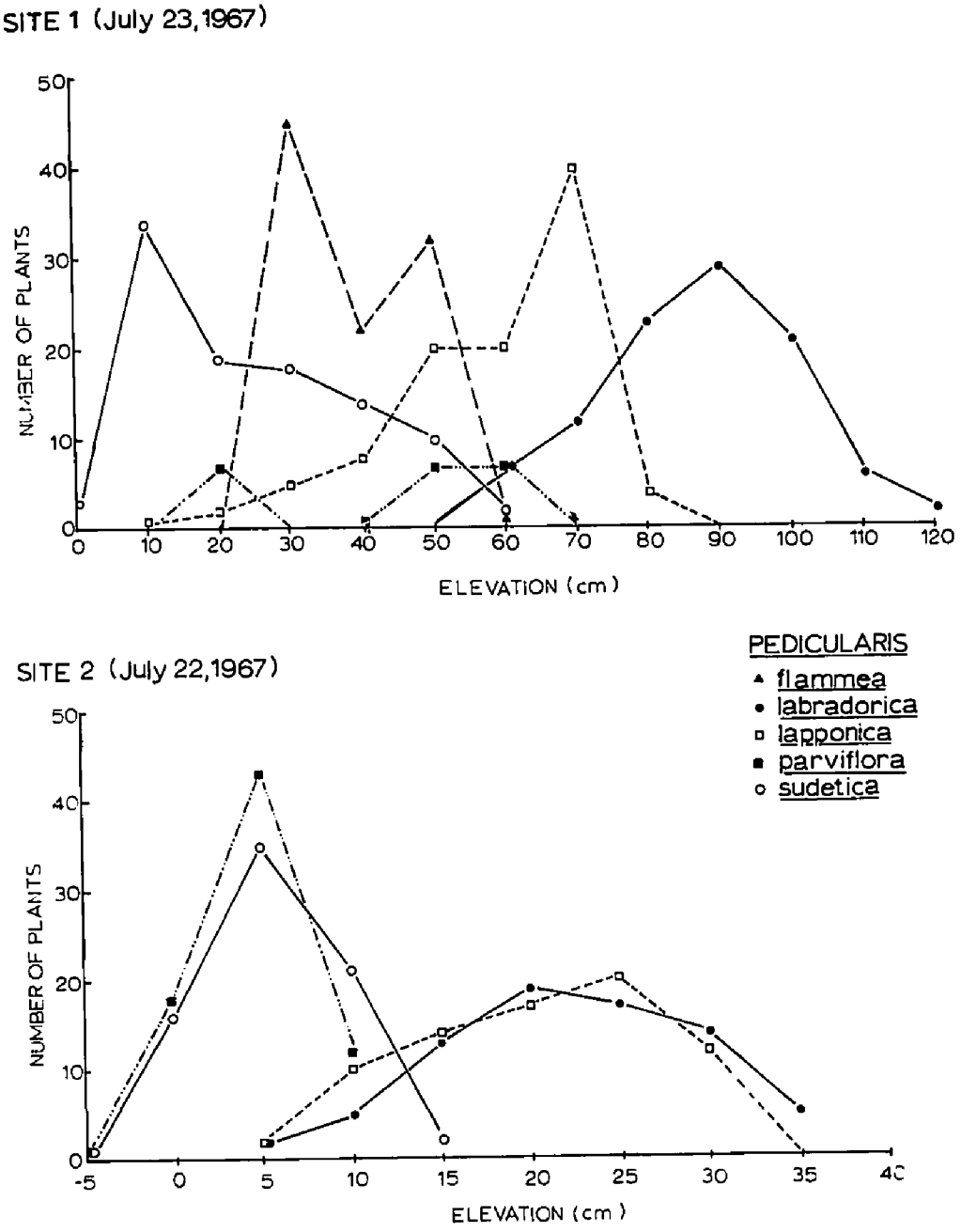

Figure 3.2-1. Microdistributions of five species of Pedicularis at the McConnell River relative to the level of open water in each of two sites.

Table 3.2-1. The number of plants of four species of Pedicularis present in 1/2 m^2 quadrats.[1]

PEDICULARIS	NUMBER OF QUADRATS	NUMBER OF PLANTS RANGE	MEAN
flammea	10	1-7	2.5
labradorica	10	1-3	1.5
parviflora	10	1-2	1.3
sudetica	10	1-4	1.7

[1] See text for explanation.

of the sampled species present.

3.3 Hemiparasitism

Plants in the genus Pedicularis contain chlorophyll but the species which have been examined also have root attachments to other plants (Wettstein 1891, Kerner 1894-1895, Volkart 1899, Maybrook 1917, Boeshore 1920, Mathiesen 1921, Sprague 1960, 1962a, Piehl 1963, 1965, and others). The haustoria produced by the roots of Pedicularis make xylem contact with the host through vessels or possibly vessels and tracheids (Sprague 1960, 1962a, Piehl 1963, 1965, Kuijt 1969). On the assumption that both the chlorophyll and the root grafts are functional, plants in the genus have been designated as hemiparasites, or semiparasites (Govier 1966, Govier et al. 1967, Atsatt and Strong 1970, Kuijt 1969). Piehl (1963) observed the passage of a stain, eosin Y, from a host to a plant of Pedicularis canadensis but no demonstration of the transfer

of organic materials such as amino acids has yet been attempted in species of Pedicularis.

One advantage of haustorial attachments is presumed to be a greater water and mineral supply for the hemiparasite, resulting from the increased root system available for absorption (Sprague 1962a). Another advantage is the opportunity for a hemiparasite to absorb and assimilate compounds such as amides and amino acids which are elaborated in the host (e.g. in Odontites verna, Govier 1966, Govier et al. 1967). However, hemiparasites may not necessarily derive benefit, or equal benefit, from all hosts (e.g. in Euphrasia spp., Wilkins 1963; in Odontites verna, Govier 1966; in Bellardia trixago, Atsatt and Strong 1970). The hosts may affect the time of flowering and the size of the inflorescence; hosts may also buffer otherwise sublethal to lethal genotypes (Atsatt 1970, Atsatt and Strong 1970).

In addition, hemiparasitic relationships may influence the distribution of plants such as Pedicularis: for example, if a host's presence is required for seed germination or subsequent seedling survival, the distribution of the hemiparasite may be restricted by the ecological tolerances of the host. Conversely, haustorial connections on a broad range of hosts may enable hemiparasites to exist under a greater variety of conditions as hemiparasites than as autotrophs.

Observations of Volkart (1899) and Piehl (1963, 1965) have shown that plants of the species of Pedicularis which

they examined did not require specific hosts. For example, Piehl (1965) found plants of Pedicularis lanceolata attached to host plants in 16 families of angiosperms. A host specificity among some species or subspecies of Pedicularis suggested by Sprague (1962a) may represent an association of two species due to the similarity of their ecological requirements rather than specific hemiparasite-host requirements (Piehl 1965).

The root systems of plants of Pedicularis were examined at the McConnell River and at Churchill to verify whether these populations of the species had attachments to the roots of other plants. If the plants did have root attachments and were hemiparasitic, host-hemiparasite interactions or the absence of a host could be expected to contribute to variations in the size of plants (i.e. in the quantity of reproductive parts), in the frequency of reproductive attempts, and in the efficiency of seed production. Full details of the examination of the root systems of Pedicularis are given in Appendix E.

The observations most pertinent here are that almost all plants of all the species of Pedicularis examined at the McConnell River, at Churchill, and at other locations in northern Manitoba, had haustorial connections to other plants when they were sampled (Tables E-1 and E-2). The exceptions are discussed in Appendix E. Assuming the haustoria are functional, it appears that most plants of Pedicularis are hemiparasitic during part, if not

throughout, their adult (post-germination) life at these locations. The host species of Pedicularis at the McConnell River are given in Appendix E.

Chapter 4

REPRODUCTION

4.1 Vegetative propagation

Vegetative propagation was observed in only one species of Pedicularis at the McConnell River. This one species, Pedicularis lapponica, was rhizomatous. Although clonal development has been reported in some plants of Pedicularis flammea and P. sudetica in other areas (resulting from independent development of lateral shoots following decay of the parent stem and root, Mathiesen 1921), it was not observed in any of the plants whose root systems were closely examined at the McConnell River (i.e. in the study root systems, Appendix E).

The presence of vegetative reproduction in one of the five species of Pedicularis represents an important difference in the strategy (Harper 1967) of reproduction; four species must reproduce at the McConnell River entirely by means of seeds, the fifth species can reproduce at the McConnell River by seeds or rhizomes or both. Although the genus Pedicularis was chosen for study because it included five species which reproduced by seeds, it is nevertheless noteworthy that vegetative propagation occurs in only one of the species because vegetative propagation is considered to be widespread in perennial angiosperms in general

(Gustafsson 1946-1947) and especially widespread in perennial angiosperms in the arctic (Billings and Mooney 1968). (The perennial character of these species will be discussed further in the last section of this chapter.)

4.2 The inflorescences and the flowers

The inflorescences of the five species of Pedicularis at the McConnell River tended initially to be capitate to subcapitate. Then as the rachis elongated during flowering and the buds and flowers became less clustered, the inflorescences became more racemose or spike-like. Depending on the species, the inflorescences were unbranched only, or unbranched and branched; and the plants possessed one only, or one or more inflorescences per plant, or per node of the rhizome (Table 4.2-1).

The corolla of the flower in the species studied here and in Pedicularis in general is zygomorphic and consists of a basal corolla tube, a hood or galea, and a three-lobed lower lip (see Figure 8.2-3). The colors and the relative sizes of the corollas of the species at the McConnell River are summarized in Table 4.2-1.

The flowers are bisexual; each flower possesses four stamens, one style, and a subcapitate stigma. The stigma may be located either inside or outside of the galea. The outside, or exsert, position is illustrated in Figure 8.2-3. The stigma is generally outside the galea in mature flowers (i.e. flowers in anthesis, as indicated by the unfolded

Table 4.2-1. Selected characteristics of the inflorescences and flowers of the five species of Pedicularis at the McConnell River.

CHARACTERISTIC	PEDICULARIS				
	FLAMMEA	LABRADORICA	LAPPONICA	PARVIFLORA	SUDETICA
Inflorescence structure	unbranched only	branched or unbranched	unbranched only	branched or unbranched	unbranched only
Number of floral stems per plant	1 - 3	1	1 - 2	1	1 - 12
Number of flowers per stem	2 - 13	2 - 465	1 - 15	3 - 308	3 - 36
Total corolla length (mm)[1].	11 - 14	14 - 17	10 - 15	12 - 16	17 - 21
Corolla tube length (mm)[2].	7 - 9	6 - 9	5 - 9	6 - 9	10 - 12
Corolla color[3].	yellow, with reddish brown on the top of the galea	yellow, with some brown on the galea	pale yellow	purple-pink-rarely white	purple-pink-rarely white
Nectar	absent	present	present	present	present
Scent[3].	absent	present	present	present	present
Stigma position	inside galea	outside galea	outside galea	outside galea	outside galea

1. Measured from fresh flowers of 20 to 30 plants per species.
2. Measured from the base of the corolla to the point of separation of the lower lip and galea on the left side of the flower.
3. From human viewpoint.

position of the lower lip) of all the species except Pedicularis flammea at the McConnell River (Table 4.2-1).

The anthers are located inside the galea and are usually paired and pressed together in such a way that they dehisce toward each other, keeping the pollen held between them. Kerner (1894-1895) aptly described the anthers as the "sprinkling variety with the sugar tong modification". Pollen can be released by dilating or shaking the galea so that the dehisced anthers separate from each other. Preliminary estimates of the proportion of stained (presumably viable) pollen grains suggested that the average pollen viability of all five species at the McConnell River was high (81% to 95%) in 1968, the only year when it was possible to conduct a microscopic examination of pollen in the field (see Appendix D).

The flowers of four species of Pedicularis also possessed both nectar and fragrance (i.e. a fragrance detectable by humans) at the McConnell River (Table 4.2-1); however, nectar and scent may not occur in all populations of these species. For example, nectar was observed in Pedicularis lapponica in Norway (Lagerberg, Holmboe, and Nordhagen 1957) and in P. sudetica at Lake Hazen, Ellesmere Island, N.W.T., Canada (Hocking 1968), but it was not observed in P. sudetica on Melville Island, N.W.T., Canada (Mosquin and Martin 1967). The flowers of Pedicularis sudetica and P. labradorica have been reported as scented in some locations (e.g. P. sudetica: Novaya Zemlya, Ekstam in

Mathiesen 1921; Greenland, Knuth 1906-1909; P. labradorica: Greenland, Mathiesen 1921) and non-scented in others (P. sudetica: Melville Island, N.W.T., Mosquin and Martin 1967; P. labradorica: Canadian Arctic Archipelago, Porsild 1964).

In Pedicularis flammea, the one species with the stigma normally inside the galea of a flower, the stigma was below and in contact with the anthers. After the anthers of a flower of P. flammea had dehisced, abundant pollen could readily be seen on the adjacent stigma and self-pollination (referring to pollen transport only, not fertilization) appeared to be inevitable.

In the remaining four species of Pedicularis, the stigma of a flower was not in direct contact with the anthers. It was not possible, however, to discern simply by observation of a flower whether the separation of the anthers and the stigma (i.e. herkogamy) was effective in preventing all pollen transport between them. A few exceptions to the usual stigma position also have been observed in these four species at the McConnell River: the different stigma positions would appear to facilitate self-pollination. For example, the stigma has been observed inside the galea near the anthers during the first or second day of anthesis in a few plants of Pedicularis labradorica and throughout anthesis in a few plants of P. lapponica, P. parviflora and P. sudetica. Occasionally, the anthers are found outside the galea of a flower,

usually in flowers with damaged corollas.

According to Sprague (1960, 1962a), Faegri and van der Pijl (1966) and Macior (1968a, 1968b, 1969, 1970), the features of flowers in the genus Pedicularis which are important in flower-pollinator relationships include the following: (1) the basic design of a "gullet type" flower with restricted access to nectar (if present) and pollen, (2) spatial separation of anthers and stigma, (3) asymmetry of flowers which limits or guides visitor movements, (4) a lip of the flower on which visitors can alight and (5) a scent. The flowers of Pedicularis at the McConnell River appear to possess all these features with the exception of the flowers of Pedicularis flammea (Table 4.2-1).

The absence of nectar and scent and the lack of separation between anthers and stigma, as in Pedicularis flammea, are characteristics commonly associated with selfing in plants, whereas the five characteristics listed in the previous paragraph, and found in the other four species of Pedicularis at the McConnell River, are associated with outcrossing, or xenogamy (Faegri and van der Pijl 1966, Ornduff 1969). Mosquin (1966) hypothesized that the specialized outcrossing features of the flowers of species of Pedicularis and of other species of Scrophulariaceae in northern Canada are largely vestigial, representing ancestral outcrossing rather than adaptations to the existing environment. This hypothesis will be considered in Chapter 8 in connection with observations on

pollination and seed production.

4.3 Phenology of flowering and fruiting

Observations related to the phenology of flowering and fruiting were made daily in the study area adjacent to the base camp at the McConnell River (km^2 03, 04, 13 and 14, Figure B-1) and involved at least several hundred plants per species. From these observations I recorded for each species, the duration of the flowering period (i.e. the time during which flowers were found in anthesis on any plants of that species) and the date of the initiation of fruit maturation (i.e. when the first dehisced capsule of a species was found). In 1966, the dates of first flowering for Pedicularis flammea and P. lapponica at the McConnell River were noted by C. D. MacInnes.

The following points concerning flowering and fruiting are of interest here. Flowering was generally initiated in all species during the first three weeks in July and generally terminated during late July and early August (Figure 4.3-1). Exceptions to this generalization included two species which began to flower on 22 July and 27 July, 1968 (Pedicularis labradorica, P. parviflora), and two species which continued to flower in mid-August of the same year (P. parviflora, P. sudetica). Another exception, not shown in Figure 4.3-1 because it involved only four plants, occurred in Pedicularis labradorica: four plants initiated flowering on 14 August, 1966, 15 days after all other plants of the species had completed flowering.

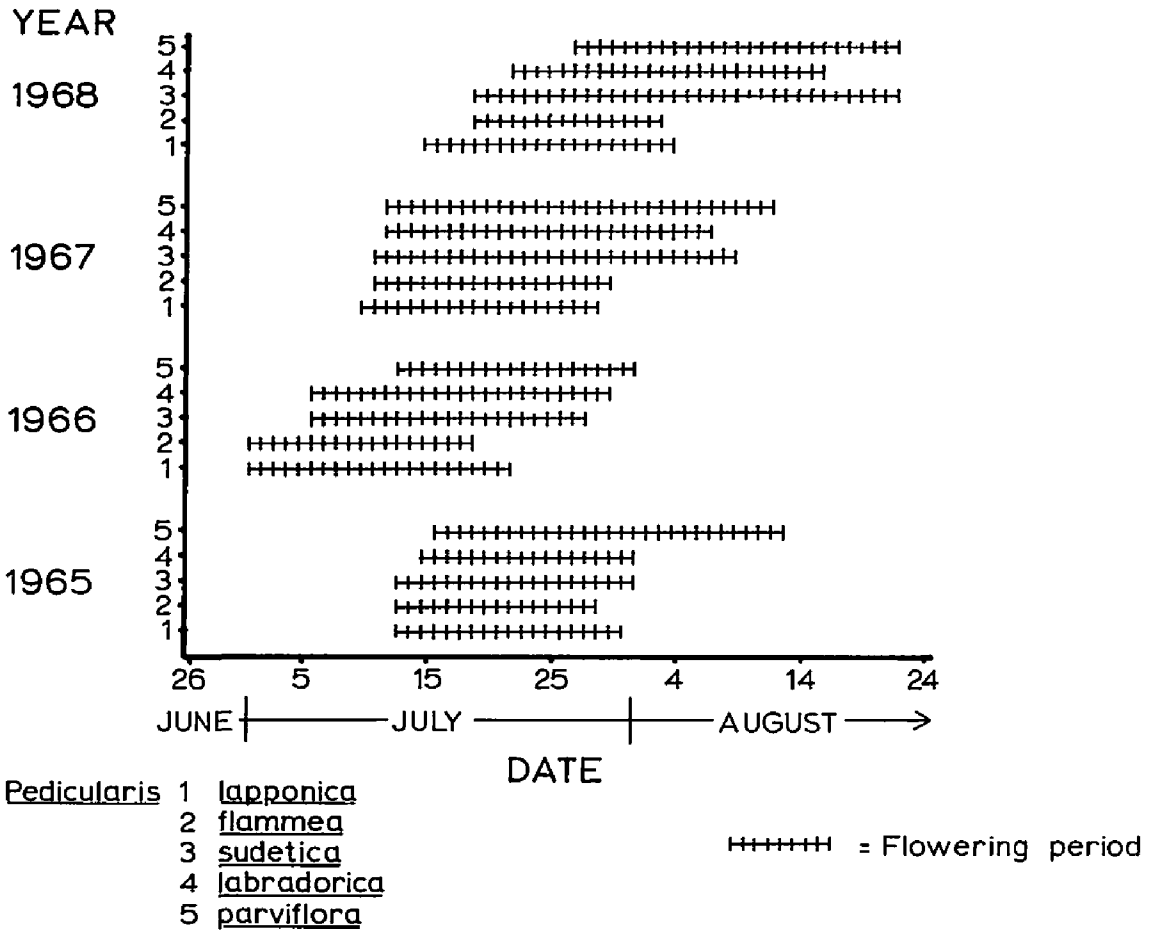

Figure 4.3-1. Flowering periods of five species of Pedicularis at the McConnell River.

The difference among the dates of first flowering for any one species of Pedicularis at the McConnell River was 13 to 18 days. The general delay in first flowering in 1968, in contrast to 1966, is partly attributed to the prolonged presence of snow, followed by extensive flooding of the study area in 1968. The snow cover was greater than 50% until 8 June, 1968, and the ground surface along the snow-cover transect was 100% water-covered on 17 June, 1968; in 1966, the snow cover was less than 50% after 30 May and the ground surface was less than 50% water-covered by 17 June (see Appendix B). In addition, June 1966, as indicated by the mean maximum air temperature (18 C, 1966; 12 C, 1968), was probably warmer than June 1968. Table 4.3-1 shows some of the variation in dates of flowering in other populations of four of the species of Pedicularis studied at the McConnell River.

The periods of flowering were similar at the McConnell River: anthesis in all five species overlapped between 6 (1966) and 17 (1967) days per year. The only days with one species flowering by itself occurred when flowering in Pedicularis lapponica preceded that in the other species (a total of five days in four years) and when flowering in P. parviflora continued after the other species had ceased (a total of 17 days in three years).

Capsule dehiscence (and subsequent release of seeds) in each species was generally initiated from late July through August, within the field period at the McConnell River except

Table 4.3-1. Examples of dates of flowering in other populations of four of the species of Pedicularis studied at the McConnell River.

PEDICULARIS	COMMENTS AND REFERENCE	
lapponica	ceased flowering about 1 August (1946); in nearby highlands, still in bloom on 10 August (1946); Greenland (67°N, 51°W)	Böcher 1952
	flowering from 10 July to 30 July (1935); Greenland (74°N, 21°W)	Sørensen 1941
flammea	flowering from 22 June to 16 July (1935); Greenland (74°N, 21°W)	Sørensen 1941
labradorica	earliest date of first flowering, 17 June; latest, 30 June; average 25 June (1962-1967); central Alaska (65°N, 145°W); U.S.A., elevation: 2,500-4,400 feet (770-1360 m)	Weeden 1968
	full bloom at the end of July (1946); Greenland (67°N, 51°W)	Böcher 1952
sudetica	earliest date of first flowering, 17 June; latest, 28 June; average, 20 June (1962-1967) Central Alaska (65°N, 145°W), U.S.A.	Weeden 1968
	first flowering on 16 June (1944); SE Yukon (60°-65°N, 133°W) Canada	Porsild 1951b
	first flowering on 18 July (1964);[1] Ellesmere Island, N.W.T. (81°N, 77°W) Canada.	Brassard personal communication
	date of full bloom, 17 August (1969); Colorado, U.S.A. (39°N, 160°W); elevation: 12,800 feet (3940 m)	Macior 1970

1. First flowering of Pedicularis sudetica at the McConnell River in 1964 occurred on 8 July.

for two species (Pedicularis sudetica, P. parviflora) in 1968 (Table 4.3-2). Thus, at the species level there was no indication that the short duration of the growing season at the McConnell River precluded seed production in Pedicularis flammea, P. labradorica, and P. lapponica in any of the years of this study (1965 through 1968), or in P. sudetica and P. parviflora in three out of four years of the study (1965 through 1967). On 20 August, 1968, the developing seeds of P. sudetica and P. parviflora examined in the oldest capsules on plants of the insect exclusion study (Chapter 8) were similar in size to mature seeds (i.e. those normally released from the plants in other years) although they were still attached to the placenta and were unpigmented. The time required for the maturation of these seeds is unknown; it is also unknown, unfortunately, whether the delay in flowering and fruiting led to a failure of seed production in Pedicularis sudetica and P. parviflora in 1968.

At the individual plant level, the only late-flowering plants that could be examined in the year after flowering were the four plants of Pedicularis labradorica, mentioned earlier, which initiated flowering on 14 August, 1966. These plants, marked and re-examined in 1967, had not produced any fruit in 1966 (their only reproductive attempt). Their failure to fruit may have been due to the shortness of the season (i.e. due to the lack of time to complete development) or to other conditions in late August and early

Table 4.3-2. The dates of first capsule dehiscence of Pedicularis species at the McConnell River.

PEDICULARIS	AUGUST 1965	1966	1967	1968
lapponica	15	(29 July)	11	19
flammea	15	2	12	20
sudetica	17	6	17	--[1].
labradorica	17	4	12	20
parviflora	18	8	18	--[1].

1. No capsules had dehisced when field work was terminated on 21 August.

September which were unfavorable for pollination, fertilization, or capsule development. Judging from the rarity and consequence of late flowering, such as in these plants of P. labradorica, there is and has been strong selection pressure for relatively early flowering in plants of Pedicularis at the McConnell River.

4.4 Longevity and the frequency of reproductive attempts

I observed plants of Pedicularis to determine if they flowered more than once, at what age they flowered first, and, if applicable, the frequency of flowering, in order to assess the importance for the individual plant of the success or failure of a single attempt at reproduction and to determine whether the species differed in their

reproductive behavior. These observations were obtained or inferred from plants which developed from seeds sown into field plots at the McConnell River (see Appendix F) and from the randomly marked plants of the reproductive survey (see Section 2.3) at the McConnell River (1966 through 1968) and at Churchill (1966 through 1967 or 1968). A more thorough determination of the age structure of the species studied was not attempted at the McConnell River since the reliability of estimates of plant ages could not be evaluated by comparisons with plants of known age.

The data in Table 4.4-1 show that none of the plants which germinated from seeds sown in plots on the tundra at the McConnell River flowered in its first year (the same calendar year as germination) in either 1967 or 1968. Only one plant of one species (Pedicularis parviflora) flowered in the second year (1967-1968). This tentatively sets the minimum length of the pre-reproductive period as two years for almost all plants of Pedicularis at the McConnell River: the species at the McConnell River were therefore classed as perennials (i.e. longevity greater than two years).

These observations from the McConnell River concur with the perennial life span normally cited for Pedicularis flammea, P. lapponica, and P. sudetica (e.g. Polunin 1959, Porsild 1964). They differ from the annual and biennial life spans cited (in floras) for P. labradorica and P. parviflora in North America (e.g. Rydberg 1932, Hultén

Table 4.4-1. The total number of vegetative and flowering plants among one-year old (year of germination) and two-year old plants developed from seeds sown into field plots at the McConnell River.

	ONE-YEAR OLD PLANTS (1967 or 1968)		TWO-YEAR OLD PLANTS (1967 and 1968)	
PEDICULARIS	VEGETATIVE	FLOWERING	VEGETATIVE	FLOWERING
flammea	789	0	204	0
labradorica	441	0	29	0
lapponica	60	0	19	0
parviflora	110	0	12	1
sudetica	26	0	19	0

1941-1950, Polunin 1959, Porsild 1964). However, both biennial and perennial life spans have been noted in plants of Pedicularis labradorica in Greenland (Mathiesen 1921, Böcher 1952, Böcher, Holmen and Jakobsen 1968).

Because of the time taken to reach first flowering, the frequency of reproductive attempts was observed and inferred from the plants of unknown age in the reproductive survey. The marked plants were scored according to the following types of seasonal development: vegetative rosette only (V), flowering (F), or dead (M). Observations of mortality were confirmed in the year following the original scoring (except after 1968) to avoid confusion with senescence of

the floral shoot. When plants were marked in 1966, stem or capsule remains from previous reproductive attempts were noted, if present. The types of seasonal development were then listed in sequence for two or three years and the frequency of plants showing a particular sequence (FFF, FFM, VFM etc.) was calculated.

In order to differentiate between longevity and the number of reproductive attempts, the term perennial was used to refer to longevity only. Plants which attempted reproduction once were called monocarpic; those which attempted reproduction more than once were called polycarpic (cf. Molish 1938, Salisbury 1942, Hillman 1962, Rabotnov 1960, 1969, Harper 1967). The five species of Pedicularis were classified into the following three categories of reproductive behavior based on the observations at the McConnell River and at Churchill.

(a) Pedicularis parviflora Invariably monocarpic.

The 100 plants marked in 1966 and the 20 plants marked in 1967 all flowered in the year in which they were marked, none of the plants survived until the following summer, and none of the plants, when marked, possessed stem or capsule remains from a prior reproductive attempt (Table 4.4-2). Therefore, it was deduced that plants of P. parviflora were monocarpic. (The absence of non-flowering plants among marked plants of the reproductive survey was undoubtedly due to their small size: they were missed in the original sampling because they were virtually impossible to

Table 4.4-2. The pattern of flowering (F) and death (M) in marked plants of Pedicularis parviflora at the McConnell River.

SITE	PATTERN	
	(1966-1967) FM	(1967-1968) FM
4	20	--
6	20	--
7	20	--
9	20	--
10	20	20[1].

1. New sample marked in 1967.

see without a centimeter by centimeter search of the ground.)

In 1967 and 1968 observations were also made on an additional 20 plants whose capsules were not harvested (i.e. the plants were "undisturbed"). The results were the same as for the plants of the reproductive survey: none of the plants flowered again.

(b) Pedicularis labradorica Primarily but not exclusively monocarpic

In this species, judged by the observations on flowering, by the absence of fruiting remains when the plants were marked and by the mortality after flowering, most plants also flowered only once at the McConnell River

(80 of 89 plants that flowered, Table 4.4-3) and at Churchill (56 of 59 plants that flowered, Table 4.4-3). A few plants at both locations flowered twice, invariably in consecutive years. There was no indication that plants flowered more than twice: none of the plants remained alive after the second year of flowering (Table 4.4-3). In one marked plant, a vegetative rosette was present in the growing season after the one in which the plant flowered; in this case, senescence was probably delayed due to the removal of the plant's inflorescence at the beginning of flowering.

Table 4.4-4 shows the frequency of plants with two reproductive attempts at the McConnell River and at Churchill: no difference was detected between locations in either 1967 (χ^2 = 1.45, ns) or 1968 (exact test, ns) or between pairs of years in either location (at the McConnell River, χ^2 = 1.9, ns; at Churchill, χ^2 = 0.4, ns). However, because of the small number of plants observed at both locations in 1968, the conclusions involving 1968 are considered to be tentative.

According to Mathiesen (1921), the majority of the plants of Pedicularis labradorica in Greenland are polycarpic. In contrast, most floras of North America cite P. labradorica as annual or biennial; thus also implying that the species is monocarpic in North America (Rydberg 1932, Hultén 1941-1950, Polunin 1959, Porsild 1964). This study indicated that polycarpy occurs in some plants at

Table 4.4-3. The patterns of flowering (F), vegetative rosette (V), and death (M) in marked plants of Pedicularis labradorica at the McConnell River and at Churchill.

(1) McConnell River

SITE	PATTERNS[1].							
	FFM	FVM	FM-	VFM	VVF	VVV	VM-	TOTAL
2	0	0	17	0	0	0	3	20
3	2	1	6	8	1	0	2	20
4	2	0	15	2	0	1	0	20
5	2	0	9	4	0	2	2	19
8	3	0	17	0	0	0	0	20
TOTAL	9	1	64	14	1	3	7	99

(2) Churchill

SITE	PATTERNS[1].					
	FFM	FM-	VFM	VVV	VM-	TOTAL
1	0	15	4	1	1	21
2	0	12	3	0	2	17
3	3	22	0	0	0	25
TOTAL	3	49	7	1	3	63

1. Patterns are given in sequence by years 1966-1967-1968.

Table 4.4-4. The frequency of plants of Pedicularis labradorica which reproduced in both 1966 and 1967 or both 1967 and 1968.

(% = plants reproducing twice / total sample X 100)

YEARS	MCCONNELL RIVER	CHURCHILL
1966-1967	9/74[1]. (12%)	3/52[1]. (6%)
1967-1968	0/14[2]. (0%)	0/7[2]. (0%)

1. Total sample equals plants flowering in 1966.
2. Total sample equals plants that were vegetative in 1966 and flowering in 1967.

two locations in North America. Additional study is needed to document whether plants in other populations of P. labradorica in North America are monocarpic or polycarpic.

(c) Pedicularis flammea — Predominantly polycarpic.
P. lapponica
P. sudetica

Table 4.4-5, which summarizes the patterns of flowering in the remaining three species (see original data in Tables A4.4-1 to A4.4-3), shows that some plants in these species flowered at least three times (P. lapponica, P. sudetica) and others flowered at least twice (all three species) during the study. In addition, most of the plants, whether they flowered once or more than once, were still

Table 4.4-5. A summary of the patterns of flowering (F), vegetative rosette (V), and death (M) in marked plants of Pedicularis flammea, P. lapponica and P. sudetica at the McConnell River and Churchill.[1].

	McConnell River			Churchill	
PEDICULARIS	1966	1967	1968	1966	1967
flammea	F (29)	- V (26)	- F (3)	F (32)	- F (2)
			- V (18)		- V (23)
			- M (5)		- M (7)
		- M (3)			
	V (69)	- F (19)	- V (15)	V (22)	- F (11)
			- M (4)		- V (11)
		- V (50)	- F (10)		
			- V (25)		
			- M (15)		
lapponica	F (76)	- F (12)	- F (4)	F (25)	- F (4)
			- V (5)		- V (12)
			- M (3)		- M (9)
		- V (49)	- F (8)		
			- V (30)		
			- M (11)		
		- M (15)			
	V (3)	- F (1)	- V (1)	V (52)	- F (4)
		- V (2)	- V (2)		- V (30)
					- M (18)
sudetica	F (70)	- F (42)	- F (31)	F (32)	- F (5)
			- V (10)		- V (15)
			- M (1)		- M (12)
		- V (28)	- F (18)		
			- V (8)		
			- M (2)		
	V (29)	- F (15)	- F (8)	V (24)	- F (8)
			- V (7)		- V (14)
		- V (14)	- F (6)		- M (2)
			- V (8)		

1. Total sample size is given in parentheses.

alive at the end of the period of observation and presumably could attempt flowering again. Therefore, these species were all classed as polycarpic.

Table 4.4-5 also shows that there was variation among species and locations in the frequency of reproductive attempts. For example, at the McConnell River numerous plants of Pedicularis sudetica flowered in two or three consecutive years, but none of the plants of P. flammea flowered in consecutive years. At Churchill, fewer plants of P. sudetica flowered in consecutive years than at the McConnell River, but some plants of P. flammea did flower in consecutive years.

In Table 4.4-6, the frequencies of plants which flowered in consecutive years are given for the four species of Pedicularis which included polycarpic plants. Comparisons between locations, pairs of years and species revealed the following significant differences in the frequency of flowering: (1) between locations in P. sudetica in 1966-1967 ($\chi^2 = 15.6$, $P<0.01$), (2) between P. sudetica and P. flammea at the McConnell River in 1966-1967 ($\chi^2 = 28.8$, $P<0.01$), in 1967-1968 ($\chi^2 = 26.3$, $P<0.01$), and in 1966-1968 ($\chi^2 = 18.7$, $P<0.01$), and (3) between P. sudetica and P. labradorica at the McConnell River in 1966-1967 ($\chi^2 = 32.2$, $P<0.01$) and in 1967-1968 ($\chi^2 = 20.7$, $P<0.01$).

In Pedicularis flammea and P. sudetica, the vegetative interval between reproductive attempts (Table 4.4-7) varied

Table 4.4-6. The proportion of plants of Pedicularis which flowered in two and three consecutive years at the McConnell River and at Churchill.[1].

PEDICULARIS	LOCATION	FLOWERED IN 2 CONSECUTIVE YEARS 1966-1967 F/N	(%)	1967-1968 F/N	(%)	FLOWERED IN 3 CONSECUTIVE YEARS 1966-1967-1968 F/N	(%)
flammea	McConnell	0/29	(0%)	0/19	(0%)	0/29	(0%)
	Churchill	2/32	(6%)	--		--	
lapponica[2].	McConnell	12/76	(16%)	4/12	(33%)	4/76	(5%)
	Churchill	4/25	(16%)	--		--	
sudetica	McConnell	42/70	(60%)	39/56	(70%)	31/70	(44%)
	Churchill	5/31	(16%)	--		--	
labradorica	McConnell	9/74	(12%)	0/14	(0%)	--	
	Churchill	3/52	(6%)	0/7	(0%)	--	

1. F = the number of plants which flowered in two or all three years.
   N = the number of plants which flowered in the first of the pair or trio of years.
2. Observed at one node of the rhizome only (data not used in statistical comparisons with the other species).

Table 4.4-7. The patterns of flowering (F) and vegetative rosette (V) in Pedicularis flammea and P. sudetica at the McConnell River.

PEDICULARIS	PATTERNS 1966-1967-1968 FFF	FFV	FVF	FVV	TOTAL[1].	F-VVV[2].
flammea	0	0	3	18	21	3
sudetica	31	10	18	8	67	2

1. Total equals the numbers of plants which flowered in 1966 and survived through 1968.
2. Plants which flowered before 1966.

from one year (FVF) to three or more years (F-VVV), assuming flowering occurs again in the latter group of plants. Eighty-six percent of the plants of Pedicularis flammea which survived all three years flowered only once (18 out of 21) in the three years (Table 4.4-7). In contrast, only 12% of the plants of Pedicularis sudetica flowered as infrequently as once in three years (8 out of 67); 42% of the plants of P. sudetica flowered in two out of three years (28 of 67), 46% of the plants flowered each year (Table 4.4-7).

Although the observations obtained here relating to longevity and the frequency of reproductive attempts give only a partial picture of the life histories of these species, they are sufficient to show that there is a major difference in reproductive behavior among the species of Pedicularis at the McConnell River. This major difference is associated with monocarpy and polycarpy. Clearly, the fate of a single reproductive attempt is more critical for all individuals of Pedicularis parviflora and most individual plants of P. labradorica because they attempt to reproduce only once, than it is for the plants of P. flammea, P. lapponica and P. sudetica, which usually make several to many attempts to reproduce.

It is generally assumed that several attempts at seed production are necessary in arctic plants which depend upon seed production for propagation, since a single attempt may be unsuccessful (Porsild 1951a, Billings and Mooney

1968). The exceptions usually cited are the few annual (obviously monocarpic) species, which may constitute only 1% to 2% of the arctic vascular flora (Billings and Mooney 1968). A second class of exceptions, encountered here, is the monocarpic perennial. Monocarpic perennials have the advantage of a longer period of development before flowering (with the potential of producing more flowers) in contrast to annuals, and of a more rapid turnover in the population (with the potential of more rapid genetic changes) in contrast to the longer-lived polycarpic perennials.

Although the fate of a single reproductive attempt is crucial for individual plants of Pedicularis parviflora and for most individual plants of P. labradorica, failure of the entire seed crop in an unfavorable season would affect only the proportion of these populations (seeds plus adult plants) which attempted flowering in that year. Thus, as in the polycarpic perennial species, extermination of the local populations of monocarpic perennials (excluding immigrant seeds) would require a series of unfavorable years for seed production as well as for germination and seedling establishment.

Intervals of one or more years between flowering attempts in other polycarpic perennials have been reported in arctic and non-arctic areas (e.g. one to four years in Ledum palustre, alternate years in Cassiope hypnoides, Warming 1908; alternate years in Pedicularis hirsuta and Ranunculus affinis, Sørensen 1941; one to four years in

Orchis mascula and Filipendula hexapetala, Tamm 1948, 1956; up to four years in Chionochloa rigida, Connor 1966, Mark 1965, 1968; one or more years in Thlaspi alpestre, Rochow 1970). The frequency of reproduction in these plants appears to depend on the species, on nutrition and on climate or location (Billings and Mooney 1968, Rabotnov 1960, 1969). According to Billings and Mooney, both the formation of floral primordia and flowering in arctic and alpine population of Oxyria digyna are related to carbohydrate levels. In species of Pedicularis, host interactions might also be expected to affect the frequency of reproduction.

Chapter 5

POTENTIAL SEED PRODUCTION

Plants of Pedicularis possess variable numbers of flowers and variable numbers of ovules within each ovary (1 ovary = 2 locules) which could become fruits and seeds. The quantities of flowers and ovules per plant were determined in 1967 and 1968, respectively, and combined to estimate an average potential seed production for each species of Pedicularis at the McConnell River.

5.1 Number of flowers per plant

The numbers of flowers per plant were estimated from random samples of plants examined at the McConnell River in 1967. In Pedicularis flammea, P. labradorica and P. parviflora, I counted the total number of flowers per plant, in P. lapponica I counted the number of flowers per node, and in P. sudetica I counted the number of stems (inflorescences) per plant and the number of flowers on one randomly selected stem from each plant. The mean number of flowers per plant of P. sudetica is the product of the mean number of stems and the mean number of flowers per stem. The term flower represents an open flower or a flower bud with the corolla visible at the apex.

The variation among species in the mean number of

flowers per plant is clearly seen in Table 5.1-1 for all the species except Pedicularis lapponica. The average number of flowers for an entire plant of P. lapponica could range from few (<10, as in P. flammea) to many (>30, as in P. sudetica, P. parviflora and P. labradorica), depending on the number of nodes with inflorescences.

The frequency distributions of all the variables given in Table 5.1-1 were significantly skewed to the right (i.e. the right tail of the curve was drawn out more than the left tail), indicating that there were relatively few plants of each species with large numbers of flowers or stems. Similarly skewed frequency distributions of growth characteristics (e.g. dry weight, capsules per plant, seeds per capsule) measured on an arithmetic scale are common in plants (cf. Obeid, Machin, and Harper 1967, Koyama and Kira 1956).

Statistical comparisons of variances and means were made among the three species in which the number of flowers was counted on each entire plant. A square root scale was used for the comparisons because the frequency distributions of values for flower number were not significantly skewed on the square root scale (Table A5.1-1). The results presented in Table 5.1-2 show that there were no significant differences between Pedicularis labradorica and P. parviflora, but each of these species differed significantly in variance and mean from P. flammea.

Table 5.1-1. Estimates of the numbers of flowers per plant of Pedicularis at the McConnell River in 1967.

PEDICULARIS	SAMPLE SIZE	FLOWERS PER PLANT		ESTIMATE OF SKEWNESS[2].
		RANGE	MEAN	
flammea	141	2 - 16	7.1	0.71 ***
lapponica	234	1 - 17	8.0	0.35 *
parviflora	105	6 - 112	35.5	0.87 ***
labradorica	145	4 - 116	36.8	1.13 ***
sudetica[1].			42.9	
	(1) 215	(1 - 11)	(2.44)	2.20 ***
	(2) 215	(3 - 36)	(17.56)	0.36 **

1. Pedicularis sudetica (1) = stems per plant, (2) = flowers per stem.
2. Reference for calculations is given in Table 2.4-1.

Table 5.1-2. Comparisons of the means and variances of the number of flowers per plant in three species of Pedicularis after a square root transformation of the data[1].

PEDICULARIS	SAMPLE SIZE	NUMBER OF FLOWERS PER PLANT (TRANSFORMED DATA)	
		MEAN	VARIANCE
flammea	141	2.62	0.26
labradorica	145	6.01	2.48
parviflora	105	5.72	2.83

1. Vertical lines indicate variances (F-tests) and means (t-tests) which were not significantly different from each other (P>0.05).

5.2 Number of ovules per ovary

The number of ovules per ovary was counted in five randomly selected ovaries from each of 20 randomly selected plants per species to obtain an estimate of the mean number of ovules (per species) and to examine variation (1) among ovaries within a plant, (2) among plants of a species, and (3) among species. Inflorescences were collected during the first week of flowering of each species at the McConnell River in 1968; the ovules were counted with the aid of a dissecting microscope. Ovaries from very small buds with no corolla visible were excluded from the sample since observations in previous years indicated that these buds did not develop into mature flowers.

The original data in Tables A5.2-1 and A5.2-2 show that the number of ovules per ovary varied within each individual plant, except for one plant of Pedicularis lapponica with 12 ovules in each ovary sampled. Since the remaining 19 plants of P. lapponica did show variation among ovaries and their variances were homogeneous (Table 5.2-1, Part A), the plant with no variation was omitted from analyses of variance, but it was included in estimates of the overall mean and in other tests not requiring homogeneity of variance. Table 5.2-1 (Part A) also shows that the variation in numbers of ovules was homogeneous among plants within each of the remaining four species of Pedicularis.

The overall mean number of ovules (per ovary) varied from 11.4 in Pedicularis parviflora to 41.1 in P. flammea

Table 5.2-1. Bartlett's test of homogeneity of variances applied to data on ovules per ovary.

A. Comparisons within each species

PEDICULARIS	df	CHI SQUARE
flammea	19	26.72 ns
labradorica	19	27.64 ns
lapponica	18[1]	22.76 ns
parviflora	19	26.35 ns
sudetica	19	20.14 ns

1. One plant with no variance was excluded from the test.

B. Comparisons among five species

DATA	df	CHI SQUARE
Within-plant variances		
Original counts	98	202.31 ***
Transformations		
Square root	98	154.47 ***
Log_{10}	98	242.99 ***
Within-species variances (using mean per plant)	4	79.19 ***

(Table 5.2-2). Since both the within-plant variances and the within-species variances (based on the mean ovules per ovary for each plant) were highly heterogeneous among species (Table 5.2-1, Part B), the species were compared in nonparametric tests (Kruskal-Wallis test and multiple comparisons by STP, see Table 2.4-1 for references). The results of these tests showed that each species differed significantly in ovule numbers from all others (Table 5.2-3).

Within each species, there was a highly significant added variance component due to plants (Table 5.2-4). The variation among plants accounted for as much as 74% and 89%

Table 5.2-2. The number of ovules per ovary in plants of Pedicularis at the McConnell River[1].

PEDICULARIS	NUMBER OF OVULES PER OVARY		
	TOTAL RANGE (ALL OVARIES)	MEAN PER PLANT	OVERALL MEAN
parviflora	4 - 18	9.2 - 15.4	11.4
lapponica	7 - 19	9.8 - 16.2	13.1
labradorica	13 - 25	15.0 - 21.4	18.6
sudetica	12 - 50	13.4 - 44.4	34.9
flammea	24 - 58	27.6 - 50.4	41.1

1. Based on five ovaries from each of 20 plants per species (1968).

Table 5.2-3. Nonparametric multiple comparisons between species of the number of ovules per ovary, based on the mean number of ovules (per ovary) per plant.[1.]

	SUMMARY OF U_s VALUES[1.]			
PEDICULARIS	parviflora	lapponica	labradorica	sudetica
lapponica	305 *			
labradorica	399 **	394 **		
sudetica	379.5 **	391 **	380 **	
flammea	400 **	400 **	400 **	306 *

1. A posteriori multiple comparisons by STP, following significance in a Kruskal-Wallis test ($H = 85.02$, 4 df, $P<0.005$). U_s = Wilcoxon-Mann-Whitney sample statistic.

of the total variance component in Pedicularis flammea and P. sudetica, respectively (Table 5.2-5). This variability among plants reflects unknown proportions of genotypic and environmental differences between plants. The differences might include effects related to host-hemiparasite interactions, the age of the plants and the frequency of flowering. The within-plant component of variation was highest (64%) in Pedicularis parviflora, suggesting considerable developmental variability (within a genotype) in this species. These levels of variation will be considered again in Chapter 8 in connection with the breeding systems.

The quantities of ovules per ovary found in the five species of Pedicularis at the McConnell River appear to encompass as much variation in ovule number as is currently

Table 5.2-4. A summary of analyses of variance of the number of ovules per ovary.

PEDICULARIS	SOURCE OF VARIATION	df	MEAN SQUARE	F
flammea	Among plants	19	188.52	15.05 ***
	Within plants	80	12.53	
labradorica	Among plants	19	14.99	5.27 ***
	Within plants	80	2.85	
lapponica[1].	Among plants	18	18.92	7.05 ***
	Within plants	76	2.68	
parviflora	Among plants	19	12.67	3.77 ***
	Within plants	80	3.37	
sudetica	Among plants	19	283.88	43.57 ***
	Within plants	80	6.52	

1. One plant with no variance was excluded from the analysis.

known for the genus (Table 5.2-6). Although the range in ovule number found in Pedicularis lapponica at the McConnell River was greater than that found by Lange (1870-1871), this difference may simply be the consequence of different sample sizes. Since none of the authors listed in Table 5.2-6 indicated sample sizes, it is presumed that the sample sizes were small.

Table 5.2-5. A summary of variance components and coefficients of variation for the number of ovules in Pedicularis (based on analyses of variance given in Table 5.2-4).

PEDICULARIS	VARIANCE COMPONENTS		COEFFICIENT OF VARIATION[1].	
	AMONG PLANTS	WITHIN PLANTS	AMONG PLANTS	WITHIN PLANTS
parviflora	1.86 (36%)	3.36 (64%)	0.120	0.161
lapponica	3.25 (55%)	2.68 (45%)	0.138	0.125
labradorica	2.43 (54%)	2.84 (46%)	0.084	0.091
sudetica	55.47 (89%)	6.52 (11%)	0.213	0.073
flammea	35.20 (74%)	12.52 (26%)	0.144	0.086

1. Calculated by dividing the square root of the appropriate variance component by the overall mean per species (Jain, Marshall and Wu 1970).

Table 5.2-6. Other evidence on the number of ovules per ovary in species of Pedicularis.

PEDICULARIS	OVULES PER OVARY	REFERENCE
canadensis	6 - 10	Neff 1968
lapponica	ca. 12 - 14	Lange 1870-1871
incarnata	ca. 12 - 14	Lange 1870-1871
tuberosa	ca. 12 - 14	Lange 1870-1871
densiflora	10 - 20	Sprague 1960
sylvatica	24 - 26	Berg 1954
groenlandica	4 - 30	Sprague 1960
hirsuta	ca. 32 - 40	Lange 1870-1871
cadmea	ca. 32 - 40	Lange 1870-1871
carnosa	ca. 32 - 40	Lange 1870-1871

5.3 Potential seed production

The range and the mean in potential seed production were estimated for each species at the McConnell River using the minimum, maximum, and mean numbers of ovules and flowers found in 1967 and in 1968. For the purpose of these estimates, it was assumed that the numbers of ovules and flowers did not differ among years. This appears to be a reasonable assumption since samples of Pedicularis taken within one year undoubtedly included plants of different ages and of different nutritional status (including plants with different host interactions), conditions which might mask differences due to years. In addition, induction and development of the flowers in these species probably occurs over two summer seasons (Mathiesen 1921, Sørensen 1941). Hence, by the time flowers reach anthesis they have been subjected to the conditions of two years: the effects of one year could thus be modified by the effects of a second year.

The estimated mean potential seed production (per reproductive attempt) showed considerable variation (15X) among species (Table 5.3-1). At one extreme, Pedicularis lapponica may average 100 potential seeds per node of rhizome (relatively few flowers and few ovules per ovary); at the other extreme, P. sudetica may average 1,500 potential seeds per plant (more flowers and more ovules). Although plants of Pedicularis parviflora had the fewest ovules per ovary (11.4) and plants of P. flammea had the most (41.1),

Table 5.3-1. Estimated potential seed production (ovules X flowers) per reproductive attempt in Pedicularis at the McConnell River.

PEDICULARIS	FLOWERS PER PLANT (1967)		OVULES PER OVARY		POTENTIAL SEED PRODUCTION PER PLANT[1].	
	RANGE	MEAN	RANGE	MEAN	RANGE	MEAN
lapponica	1- 17	8.0	9.8-16.2	13.1	10- 270	100
flammea	2- 16	7.1	27.6-50.4	41.1	60- 810	290
parviflora	6-112	35.5	9.2-15.4	11.4	60-1,720	400
labradorica	4-116	38.6	15.0-21.4	18.6	60-2,480	720
sudetica	3-396	42.9	13.4-44.4	34.9	40-17,580	1,500

1. Rounded to the nearest 10.

their potential numbersof seeds (per plant) per reproductive attempt were relatively similar (400 to 280) because plants of P. parviflora averaged five times as many flowers as plants of P. flammea.

Chapter 6

SEED PRODUCTION AND REPRODUCTIVE EFFICIENCY

The seed production, or seed output, per reproductive attempt was determined in 1965 through 1968 from marked plants at the McConnell River by counting the seeds just before they would normally be released from the plant (see Section 2.3). In addition, counts of seeds, which represent the minimum seed output of marked plants, were made in Churchill in 1966 from those seeds remaining in capsules that had already dehisced. As indicated in Chapter 1, reproductive efficiency is an expression of the realized seed production as a percentage of the potential seed production. It provides a comparative measure of the success of seed production among the species of Pedicularis at the McConnell River: the most "successful" species was arbitrarily defined in this study as the one with the highest reproductive efficiency.

6.1 McConnell River

(a) Variation in seed output

The original count data on the number of seeds (per plant) per reproductive attempt are given in Tables A6.1-1 through A6.1-5. As indicated earlier (Section 2.3), no samples were available for Pedicularis labradorica, P. parviflora

and P. sudetica in 1968. The data on seed output were first analysed in nested analyses of variance, appropriate where subordinate levels (sites and plants) were randomly selected, following a logarithmic transformation of the data. A logarithmic transformation was used because the variances were homogeneous among sites within each of the five species of Pedicularis on this scale (see Table A6.1-6). The variation among sites within each year was examined in one-way analyses of variance. The references for all calculations are indicated in Table 2.4-1. Sites with less than five observations, and years with less than two sites with at least five observations each, were omitted from the analyses.

The examination of the variation in seed output among plants, sites, and years revealed the following results. First, there was no significant variation due to years in any of the species of Pedicularis at the McConnell River during the years which could be tested (Table 6.1-1). Thus, during this period less variation was detected between years than within years. There was, however, an indication that differences in seed output between years might sometimes occur in Pedicularis parviflora and P. sudetica at the McConnell River under conditions identical or similar to those prevailing during the years of this study. For example, if the delay of fruit maturation of Pedicularis sudetica and P. parviflora in 1968 (see Section 4.3) led to widespread reproductive failure, significant differences in seed production between years might have been detected in

Table 6.1-1. A summary of nested analyses of variance of log ($\log_{10}$ Y + 1) seeds per plant of Pedicularis at the McConnell River.

PEDICULARIS	SOURCE OF VARIATION	df	MEAN SQUARE	F
flammea	Years (1965-1967)	2	1.240	0.457 ns
	Sites	4.9	2.714	5.328 ***
	Plants	50	0.490	
labradorica	Years (1965-1967)	2	0.360	0.348 ns
	Sites	7.9	1.034	2.720 *
	Plants	108	0.418	
lapponica	Years (1965, 1966)	1	0.074	0.073 ns
	Sites	6.7	1.010	5.882 ***
	Plants	119	0.216	
parviflora	Years (1965, 1966)	1	0.178	0.102 ns
	Sites	5.3	1.755	4.156 ***
	Plants	122	0.456	
sudetica	Years (1965-1967)	2	1.537	0.493 ns
	Sites	10.0	3.119	8.531 ***
	Plants	139	0.370	

those species.

Second, there was a significant added variance component due to sites in each species (Table 6.1-1). When

each year was examined separately, the results showed that seed production differed ($P<0.05$) among sites in each year for Pedicularis sudetica and in some years (e.g. 1966) for the remaining four species (Table 6.1-2). Examples of the variation in the mean numbers of seeds per plant per site are given in Table 6.1-3 for those years in which significant differences were detected among sites (untransformed means given). The mean numbers of seeds for all sites are available in Tables A6.1-1 to A6.1-5.

The detailed examinations of marked plants in the field and of the capsules when seeds were counted revealed two conditions which might contribute to these unexpectedly large differences between randomly selected sites: (1) variation among sites in the frequencies of plants which did not complete fruit and seed production (i.e. the "incomplete reproducers") and (2) variation among sites in the frequencies of plants with damage to ovaries, ovules, capsules and seeds (i.e. the "damaged plants", Figure 2.3-1). These categories of plants will be considered in Chapter 7.

Third, variation among plants within sites was also high: it accounted for 58% to 100% of the total estimated variation in all 13 of the analyses of variance by year (Tables 6.1-2 and 6.1-4). A relatively large amount of variation was anticipated among individual plants because (1) individual plants were known to have different numbers of ovules and flowers (Chapter 5), (2) some plants observed in the field did not complete flowering or fruiting (thus

Table 6.1-2. Analyses of variance of log ($\log_{10}$ Y + 1) seeds per plant among sites and among plants (within sites).

PEDICULARIS	YEAR	SOURCE OF VARIATION	df	MEAN SQUARE	F
flammea	1965	Sites	1	3.689	6.351 *
		Plants	18	0.581	
	1966	Sites	3	2.707	5.897 **
		Plants	23	0.459	
	1967	Sites	1	1.257	3.224 ns
		Plants	9	0.390	
labradorica	1965	Sites	2	0.331	0.606 ns
		Plants	24	0.546	
	1966	Sites	4	1.427	3.600 **
		Plants	69	0.396	
	1967	Sites	1	1.594	5.074 *
		Plants	15	0.314	
lapponica	1965	Sites	2	0.545	1.926 ns
		Plants	27	0.283	
	1966	Sites	4	1.636	8.315 ***
		Plants	92	0.197	
parviflora	1965	Sites	1	0.001	0.002 ns
		Plants	27	0.424	
	1966	Sites	4	2.368	5.095 **
		Plants	95	0.465	
sudetica	1965	Sites	2	3.420	7.964 ***
		Plants	25	0.429	
	1966	Sites	4	3.891	10.225 ***
		Plants	66	0.381	
	1967	Sites	4	2.290	7.056 ***
		Plants	48	0.325	

Table 6.1-3. Examples of mean number of seeds per plant per site.

PEDICULARIS	YEAR	SITE	SAMPLE SIZE	MEAN
flammea	1965	A1	10	23.7
		A2	10	86.9
	1966	11	9	6.7
		3	7	15.4
		2	5	68.6
		1	6	104.2
labradorica	1966	4	17	24.9
		3	9	27.2
		2	17	42.0
		5	11	49.8
		8	20	73.4
	1967	5	7	12.9
		3	10	44.1
lapponica	1966	3	19	1.9
		5	18	5.0
		2	20	8.1
		8	20	10.5
		1	20	13.2
parviflora	1966	6	20	75.6
		7	20	84.5
		10	20	172.3
		4	20	205.0
		9	20	293.6
sudetica	1965	A3	8	10.9
		A1	10	20.5
		A4	10	115.5
	1966	3	8	1.1
		6	18	2.3
		1	11	15.5
		7	20	30.1
		2	14	61.2
	1967	3	11	4.8
		1	11	10.7
		6	10	31.6
		7	9	39.3
		2	12	44.8

Table 6.1-4. Estimated variance components of seed output due to sites and plants.[1].

PEDICULARIS	SOURCE OF VARIATION	YEAR 1965	1966	1967
flammea	Sites	0.31 (35%)	0.34 (42%)	0.16 (29%)
	Plants	0.58 (65%)	0.46 (58%)	0.39 (71%)
labradorica	Sites	—	0.07 (15%)	0.16 (33%)
	Plants	— (100%)	0.40 (85%)	0.31 (67%)
lapponica	Sites	0.02 (6%)	0.07 (27%)	--
	Plants	0.28 (94%)	0.19 (37%)	
parviflora	Sites	—	0.10 (17%)	--
	Plants	— (100%)	0.46 (83%)	
sudetica	Sites	0.32 (43%)	0.25 (40%)	0.19 (36%)
	Plants	0.43 (57%)	0.38 (60%)	0.32 (64%)

1. Based on the analyses of variance given in Table 6.1-2.

having no seeds per reproductive attempt), and (3) the reproductive parts of some plants were damaged. The differential seed production among individual plants within each site is readily seen in the original data (Table A6.1-1 to A6.1-5).

Another way of looking at the differential seed contribution of individual plants (assuming no cross-pollination) is to compare the plant with the largest number of seeds per site to the total number of seeds collected from all the plants sampled in the site (Table 6.1-5, sites are in the same order as in the original data tables, sites with less than three plants are excluded).

Table 6.1-5. Comparison of the number of seeds in the most fecund plant (F) per site to the total number of seeds (T) produced by the plants sampled (n) within each site (McConnell River).

	PEDICULARIS											
	FLAMMEA			LABRADORICA			LAPPONICA			PARVIFLORA			SUDETICA		
YEAR	n	F / T	(%)	n	F / T	(%)	n	F / T	(%)	n	F / T	(%)	n	F / T	(%)
1965	10	97/237	(41)	10	532/1136	(47)	10	19/95	(20)	10	557/1919	(29)	10	71/205	(35)
	10	317/869	(36)	10	110/481	(23)	10	26/115	(23)	19	882/3220	(27)	8	54/87	(62)
				7	83/240	(35)	10	32/75	(43)				10	366/1154	(32)
1966	6	220/625	(35)	17	92/714	(13)	20	39/264	(15)	20	580/4101	(14)	11	50/171	(29)
	4	159/343	(46)	9	115/245	(47)	20	26/163	(16)	20	355/1512	(23)	14	201/857	(23)
	7	84/108	(78)	17	105/423	(25)	19	11/36	(31)	20	596/1690	(35)	8	9/9	(100)
	3	94/103	(91)	11	367/548	(67)	18	24/90	(27)	20	1132/5869	(19)	18	21/41	(51)
	9	43/60	(72)	20	136/1468	(9)	20	36/211	(17)	20	884/3446	(26)	20	126/602	(21)
1967	4	206/593	(35)	10	141/441	(32)	7	6/15	(40)	5	127/213	(60)	11	50/118	(42)
	6	98/247	(40)	4	24/42	(57)	4	27/36	(75)	3	608/671	(91)	12	121/538	(22)
	3	61/141	(43)	7	35/90	(39)							11	32/53	(60)
	5	161/457	(35)	3	31/45	(69)							10	64/316	(20)
													9	95/354	(27)
1968		--			--		3	18/26	(69)		--			--	
							4	56/85	(66)						
Overall Mean %			(50)			(39)			(37)			(36)			(37)

The percentage seed contribution of the most fecund plant (i.e. the plant bearing the most seeds) per site was as high as 100% in one site. On the average, the seeds possessed by the most fecund plant contributed 36% to 39% of the total seeds collected per site in Pedicularis lapponica, P. sudetica, P. labradorica and P. parviflora, and 50% of the total seeds collected per site in P. flammea (Table 6.1-5). If seeds tend to remain in the vicinity of the seed parent after they are released, one consequence of the differential seed contribution per plant is that numerous sibling offspring could become established in a small area, resulting in micropopulations of related individuals.

The data on seed production also showed that these species of Pedicularis with their various "seed-reproducing phenotypes" (e.g. frequency of reproduction, floral morphology) were all capable of producing seeds in the presumably severe conditions at the McConnell River. This result implied that there was sufficient opportunity under the current conditions at the McConnell River for the existence and presumably the persistence of different reproductive strategies (genotypic) and tactics (phenotypic, cf. Harper and Ogden 1970) among the species and individuals of Pedicularis occurring there.

(b) Average seed production and reproductive efficiency

The range, mean, and median numbers of seeds per reproductive attempt for each species, pooled from all observations at the McConnell River (1965-1968), are seen in

Table 6.1-6. Comparisons of these values for each species again suggest the skewness of the frequency distributions of numbers of seeds per reproductive attempt. For example, although plants of Pedicularis sudetica produced an average of 30 seeds, half of the plants had nine or fewer seeds. (Tests of skewness were not conducted on the pooled data). Salisbury (1942) noted that populations of monocarpic species frequently included a high proportion of plants with few seeds: these results indicate that both the monocarpic and polycarpic species of Pedicularis had high proportions of plants with relatively few seeds at the McConnell River.

The mean number of seeds per reproductive attempt in all plants of Pedicularis parviflora and in most plants of P. labradorica also equalled the average total seed production per plant, since all plants of the former species and most plants of the latter species were monocarpic at the McConnell River. Table 6.1-6 shows that plants of P. parviflora were about three times more fecund than plants of P. labradorica. Plants of Pedicularis flammea and P. sudetica, both polycarpic species, would require two to three and five to six reproductive attempts, respectively, to average as large a total seed output as P. parviflora. Considering the frequency with which plants of P. flammea and P. sudetica flower at the McConnell River (Table 4.4-7), it might take about the same time period (about six years) for plants of both species to equal the average total seed

Table 6.1-6. The number of seeds per plant, per reproductive attempt, at the McConnell River (pooled, 1965-1968).

PEDICULARIS	SAMPLE SIZE	SEEDS PER PLANT (PER REPRODUCTIVE ATTEMPT) RANGE	MEAN	MEDIAN
lapponica[1]	147	0 - 56	8.3	5.0
sudetica	152	0 - 366	29.6	9.0
labradorica	125	0 - 532	47.0	31.0
flammea	77	0 - 405	56.6	32.0
parviflora	139	0 - 1,132	163.6	81.0

1. Plant = one node of the rhizome.

production in P. parviflora. In contrast, the average seed output in P. flammea in one season exceeds the total seed output of most plants of P. labradorica. Whether the observed seed output of any of these species of Pedicularis equals that required to maintain stable populations in the study area is unknown.

When the mean seed output is then compared to the potential seed production, reproductive efficiencies ranging from 2% in Pedicularis sudetica to 40% in Pedicularis parviflora are found (Table 6.1-7). It is noteworthy that the species with the highest potential number of seeds had the lowest reproductive efficiency. Factors contributing to reproductive failures in individual plants, and hence to the lowering of the overall reproductive

Table 6.1-7. Approximate reproductive efficiency in species of Pedicularis at the McConnell River.[1.]

PEDICULARIS	MEAN SEED OUTPUT	MEAN POTENTIAL SEED PRODUCTION	REPRODUCTIVE EFFICIENCY
sudetica	29.6	1,497.2	2%
labradorica	47.0	718.0	7%
lapponica	8.3	104.8	8%
flammea	56.6	291.8	19%
parviflora	163.6	404.7	40%

1. $\%\ \text{reproductive efficiency} = \frac{\text{mean seed output}}{\text{mean potential seed production}} \times 100$

efficiencies per species are considered in the next two chapters.

Porsild (in Mathiesen 1921) considered Pedicularis lapponica to be "the poorest fruit-setting species in Greenland". Other species of Pedicularis in Greenland which evidently appeared to have better seed-set included P. flammea and P. labradorica. In a numerical sense, if a plant of P. lapponica is delimited as one node, then plants of P. lapponica at the McConnell River would appear to have a lower seed output than the other four species of Pedicularis. However, in terms of the efficiency of fruit-setting (i.e. the reproductive efficiency), two other species of Pedicularis at the McConnell River (P. sudetica, P. flammea) had poorer fruit-set than P. lapponica.

Some estimates of the proportions of fruits or seeds produced in other plant species are listed in Table 6.1-8. These examples from temperate and tropical regions illustrate that the efficiency of fruit and seed production may also be relatively low outside the arctic.

The effectiveness of seed production depends to a considerable degree on the proportions of the seeds which are viable and therefore capable of germination. Unfortunately, the evidence of seed viability based on positive results from field germination tests (see Appendix F) gave limited information on the quality of most of the seeds produced at the McConnell River: the results of the germination tests were mostly negative even though the results of these tests produced higher percentages of germination than those previously reported for three species (Tables F-1 and F-8). Some of the negative results in these tests could have been due simply to the loss of seeds from the quadrats. The highest percentages of germination recorded in quadrats at the McConnell River using seeds collected in 1965 or 1966 indicated that the viability was at least as high as 84% in Pedicularis flammea (1965 seeds), 54% in P. labradorica (1965 seeds), 52% in P. parviflora (1966 seeds), 34% in P. lapponica (1965 seeds) and 14% in P. sudetica (1966 seeds).

6.2 Churchill

The mean number of seeds (those remaining in dehisced capsules) per plant in the four species of Pedicularis

Table 6.1-8. Examples of references which give estimates of the proportions of fruits or seeds which are produced, or, the proportions of seeds which are destroyed.

SPECIES OF PLANT	COMMENTS ON REPRODUCTION	REFERENCE
Chionochloa rigida	0 - 61% seed-set in florets	Mark 1965
Ranunculus flammula	38% - 95% of the carpels had a seed	Johnson and Cook 1968
Brassica oleracea varieties	a maximum of 70% of the ovules became seeds	Watts 1968
Acacia cornigera and other legumes	up to 100% of the seed crop destroyed	Janzen 1967, 1969
Lupinus amplus	ca. 50% of the potential seed production destroyed	Breedlove and Ehrlich 1968
Lupinus luteus	65% - 94% of the ovules became seeds	van Steveninck 1957
Pisum sativum	30% - 50% of the ovules in a pod develop to maturity	Linck 1961
Vicia faba	4% - 70% of the ovules became seeds	Rowlands 1960
Linaria vulgaris	insects, feeding on seeds, can reduce the seed output by about 90%	Harris 1963

examined at Churchill in 1966 ranged from 13.7 in Pedicularis lapponica to 93.1 in P. labradorica (Table 6.2-1). At Churchill, these species averaged from 50% (P. lapponica) to at least 300% (P. sudetica but based on a small sample)

more seeds per plant than at the McConnell River, despite the seed loss at Churchill. In addition, the maximum numbers of seeds found on the most fecund plants of Pedicularis flammea and P. labradorica at Churchill were at least two and five times higher, respectively, than on the most fecund plants of these species at the McConnell River.

Table 6.2-1. Comparisons of the numbers of seeds per plant at the McConnell River with the numbers of remaining seeds per plant at Churchill (1966).

PEDICULARIS	LOCATION	SEEDS PER PLANT SAMPLE SIZE	RANGE	MEAN
lapponica	Churchill	26	0 - 43	13.7
	McConnell	97	0 - 39	7.9
sudetica	Churchill	6	27 - 215	79.0
	McConnell	71	0 - 201	23.7
flammea	Churchill	38	0 - 447	77.9
	McConnell	30	0 - 220	41.3
labradorica	Churchill	74	0 - 672	93.1
	McConnell	74	0 - 131	45.9

Chapter 7

INCOMPLETE REPRODUCERS AND DAMAGED PLANTS

7.1 Incomplete reproducers

The incomplete reproducers were those plants which attempted reproduction but produced no seed(s), excluding plants whose seed production failed due to damage to flowers and ovules (see scoring diagram, Figure 2.3-1). Since an incomplete reproducer had no seeds, it obviously contributed to the lowering of the overall mean seed output per reproductive attempt and to a reduction in the reproductive efficiency of a species. In monocarpic plants (Pedicularis parviflora, P. labradorica) incomplete reproduction meant total seed and possibly genetic failure for the individual.

Table 7.1-1 shows the frequency of incomplete reproducers out of the total number of reproductive attempts sampled for each year at the McConnell River and at Churchill. The numbers of incomplete reproducers were pooled for years since 2 X 2 tests (exact probability) indicated that in all but three cases there were no significant differences ($P>0.05$) between sites within a year (McConnell River original data in Tables A6.1-1 to A6.1-5). In 1968, no marked plants were available for Pedicularis labradorica and no observations were recorded for P. sudetica and P. parviflora because their fruits were still immature when the field work was

terminated at the McConnell River. As indicated earlier (Section 4.3), it unfortunately is not known whether plants of P. sudetica or P. parviflora completed reproduction in that year.

The frequencies of incomplete reproducers for the three cases in which significant differences were detected between sites within a year (Pedicularis lapponica, 1966; P. sudetica, 1966 and 1967) are shown in Table 7.1-2. In Site 3 in 1966, 26% (5/19) of the reproductive attempts of Pedicularis lapponica were incomplete. The mean seed output in Site 3 that year (1.9 seeds per plant) was lower than in any of the other four sites (see Table 6.1-3); thus, the incomplete reproducers clearly contributed to the differences between sites in seed output. Similar results were found in Pedicularis sudetica: the sites with the highest frequencies of incomplete reproducers had the lowest mean seed outputs per plant of the sites sampled in those years (1966: Site 3, 1.1 seeds per plant, Site 6, 2.3 seeds per plant; 1967: Site 3, 4.8 seeds per plant; see Table 6.1-3).

The annual frequency of incomplete reproducers for any of the species ranged between 0% and 22% at the McConnell River and between 0% and 9% at Churchill (Table 7.1-1). No significant differences in the frequency of incomplete reproducers (2 X 2 tests, exact probability) were detected; (1) among years within each species at the McConnell River or at Churchill, (2) between locations within each species, (1966, 1967), or (3) among different species

Table 7.1-1. The frequency of incomplete reproducers out of the total number of reproductive attempts in marked plants of Pedicularis.

		PEDICULARIS				
LOCATION	YEAR	FLAMMEA	LABRADORICA	LAPPONICA	PARVIFLORA	SUDETICA
McConnell River	1965	0/20 (0%)	4/27 (15%)	3/30 (10%)	0/29 (0%)	4/28 (14%)
	1966	1/30 (3%)	2/74 (3%)	9/97[1] (9%)	1/100 (1%)	12/70[1] (17%)
	1967	2/19 (11%)	3/24 (12%)	1/14 (7%)	0/10 (0%)	10/52[1] (19%)
	1968	0/8 (0%)	--	2/9 (22%)	--	--
	Total	3/77 (4%)	9/125 (7%)	15/140 (11%)	1/139 (1%)	26/152 (17%)
Churchill	1966	1/38 (3%)	0/74 (0%)	1/26 (4%)	--	1/31 (3%)
	1967	0/13 (0%)	1/9 (11%)	0/8 (0%)	--	1/11 (9%)
	Total	1/51 (2%)	1/83 (1%)	1/34 (3%)		2/42 (5%)

1. Frequency differs significantly between sites (see Table 7.1-2).

within each year. (Years and species with significant differences between sites were not involved in these three sets of comparisons).

The overall frequency of incomplete reproducers (based on data for three or four years) varied from 1% in

Table 7.1-2. The frequency of incomplete reproducers of Pedicularis lapponica and P. sudetica per site in years with significant differences between sites.

						SIGNIFICANT DIFFERENCES (2 X 2 TESTS)
PEDICULARIS LAPPONICA				1966		
PLANTS	SITES					
	1	2	3	5	8	
Number of incomplete reproducers	1	2	5	1	0	Sites 3 and 8*
Total	20	20	19	18	20	
PEDICULARIS SUDETICA				1966		
PLANTS	SITES					
	1	2	3	6	7	
Number of incomplete reproducers	0	1	6	5	0	Sites 3 and 1** 3 and 2** 3 and 7*** 6 and 7*
Total	11	14	8	18	20	
				1967		
PLANTS	SITES					
	1	2	3	6	7	
Number of incomplete reproducers	1	1	7	0	1	Sites 3 and 1* 3 and 2* 3 and 6** 3 and 7*
Total	11	12	11	10	9	

Pedicularis parviflora to 17% in P. sudetica. Pedicularis parviflora and P. sudetica also had the highest (40%) and lowest (2%) reproductive efficiencies, respectively (Table 6.1-7). The overall mean number of seeds was 29.6 in P. sudetica and 163.6 in P. parviflora for all reproductive attempts compared to 35.8 and 164.8, respectively, for reproductive attempts excluding the incomplete reproducers. The difference in mean seed output per plant was 21% (6.2/29.6) in P. sudetica and less than 1% (1.2/163.6) in P. parviflora. Thus, the incomplete reproducer class of plants had a greater influence on the estimated reproductive efficiency in P. sudetica than in P. parviflora.

The inflorescences of the incomplete reproducers reached various stages of maturity before senescing. At one extreme, the inflorescences senesced before any flowers reached anthesis (Pedicularis sudetica); at the other extreme, the flowers of an inflorescence appeared to complete anthesis but the ovules did not develop into seeds (all species). Since other marked plants in the sites, going through similar stages of inflorescence development at the same time as the incomplete reproducers, produced seeds, it is unlikely that the length of the growing season per se was responsible for the reproductive failures noted here.

Reproductive failures in the plants of Pedicularis sudetica whose inflorescences aborted before floral anthesis might have been the consequence of a variety of conditions (e.g. nutritional, physiological, environmental, genetical);

but, because of the timing, the conditions presumably did not involve poor quality of pollen, inadequate or inappropriate pollination, failure of fertilization, or abortion of fertilized ovules. Reproductive failures in inflorescences during and after anthesis may have involved any of these conditions just mentioned. The relationships between pollination, fertility, and seed-set will be examined further in the following chapter. It is not clear why a high proportion of inflorescences of both Pedicularis lapponica and P. sudetica in Site 3 failed to complete reproduction.

7.2 Damaged plants: capsule and seed predation

Two types of damage were noted in the marked plants of the reproductive survey: (1) the loss of flowers or developing capsules, (designated as capsule predation) and (2) the loss of ovules and developing seeds within individual ovaries and capsules (designated as seed predation). Ovaries and ovules were arbitrarily delimited from capsules and seeds to distinguish the relative timing of the fruit development and of the damage: an ovary (which usually contained ovules) became a capsule (which may have contained developing seeds) when the enlarged ovary was greater in length than the calyx. Additional collections of plants were examined in 1968 to determine the locations of insect larvae on plants. Insect larvae, puparia, and adults were identified by G. E. Shewell and J. R. Vockeroth of the Entomology Research Institute, Canada Department of Agriculture, Ottawa. Reference

specimens of the insects are available in the Canadian National Collection (CNC), Ottawa.

The two types of damage described above were termed predation because the damage resulted in the destruction of potential seeds, or potential plants (sensu Janzen 1970). The following aspects of predation are considered in this study: (1) the frequency of damaged reproductive attempts, (2) the types of damage and the predators, and (3) the effects of this predation on seed production.

7.21 The frequency of damaged reproductive attempts

Damage was found in all five species of Pedicularis in most years at both the McConnell River and at Churchill (summarized by years in Table 7.21-1, original data in Tables A7.21-1 and A7.21-2). Up to 85% of the reproductive attempts sampled in one year (excluding the incomplete reproducers) were predated (Pedicularis sudetica, 1966).

Variation in the frequency of damage was detected at four levels: sites, years, locations and species. However, significant differences in the frequency of damaged plants among sites, within a year, were found in only 3 out of 25 sets of data (Table 7.21-1), thus suggesting that the frequency of damaged plants is relatively uniform throughout the sites in a particular year. The exceptions to this uniformity are shown in Table 7.21-2. (This table includes only the sites which differed significantly.) All significant differences between years, locations, and

Table 7.21-1. The frequency of damaged (D) and undamaged (UD) reproductive attempts in marked plants of Pedicularis.[1]

LOCATION	YEAR	PEDICULARIS FLAMMEA D	UD	LABRADORICA D	UD	LAPPONICA D	UD	PARVIFLORA D	UD	SUDETICA D	UD
McConnell	1965	(13	7)	4	19	7	20	8	21	18	6
		65%		17%		26%		28%		75%	
	1966	21	8	36	36	24	64	47	53	50	9
		72%		50%		27%		47%		85%	
	1967	0	17	1	20	3	10	3	7	(9	34)
		0%		5%		23%		30%		21%	
	1968	4	4	--		0	7	--		--	
		50%				0%					
Churchill	1966	17	20	17	57	9	16	--		(23	7)
		46%		23%		36%				77%	
		7	6	4	4	1	7	--		7	3
		54%		50%		13%				70%	

1. The data from sites are pooled within years; parentheses indicate years with significant differences between sites (see Table 7.21-2). The percentage of damaged attempts out of the total (D + UD) attempts per year is given.

species are summarized in Table 7.21-3. These differences in the frequency of damaged plants may reflect differences in a combination of factors such as the kinds and specificities of predators, the proximity or mobility of predators, the plant density, and the timing of plant development relative to animal feeding or egg laying (cf. Neff 1968, Singer 1971).

The overall frequency of damaged reproductive attempts at the McConnell River for all years ranged from 26% in

Table 7.21-2. Sites within years which differed significantly in the frequencies of marked plants with damage[1].

LOCATION	YEAR	PEDICULARIS FLAMMEA				PEDICULARIS SUDETICA			
		SITE	D	UD		SITE	D	UD	
McConnell	1965	A1	10	0	**	1967	1	0	10	*
		A2	3	7			6	0	10	*
							7	4	4	
Churchill						1966	1	0	5	**
							2	4	1	
							4	19	1	

1. 2 X 2 tests (exact probability); D = damaged plants, UD = undamaged plants.

Pedicularis lapponica to 61% in Pedicularis sudetica (Table 7.21-4). These frequencies of damage occurred despite the activities of humans within the study area: if herbivore (i.e. seed or capsule predator) feeding was adversely affected by human activity, these may represent conservative estimates of damage.

Table 7.21-3. A summary of the significant differences in the frequency of marked plants with damage.[1].

COMPARISONS		SIGNIFICANT DIFFERENCES
Within species		
between years	*Pedicularis flammea*	
	McConnell	1966 and 1967 **
		1967 and 1968 **
	P. labradorica	
	McConnell	1965 and 1966 *
		1966 and 1967 **
between locations	*P. flammea*	1967 McConnell and Churchill **
	P. labradorica	1966 McConnell and Churchill **
		1967 McConnell and Churchill *
Between species		
McConnell River	1965	*P. sudetica* and *P. labradorica* **
		P. sudetica and *P. lapponica* **
		P. sudetica and *P. parviflora* **
	1966	all comparisons except *P. sudetica* and *P. flammea* *P. labradorica* and *P. parviflora*
Churchill	1966	*P. flammea* and *P. labradorica* *
	1967	*P. lapponica* and *P. sudetica* *

1. 2 X 2 tests. Tests between years, locations and species were not conducted using data from years in which there were significant differences between sites (Table 7.21-2).

Table 7.21-4. Overall frequencies of damaged reproductive attempts out of the total damaged and undamaged attempts at the McConnell River, 1965-1968.

PEDICULARIS	REPRODUCTIVE ATTEMPTS: TOTAL DAMAGED AND UNDAMAGED ATTEMPTS	REPRODUCTIVE ATTEMPTS: DAMAGED ATTEMPTS
lapponica	132	34 (26%)
labradorica	116	41 (35%)
parviflora	138	58 (42%)
flammea	74	38 (51%)
sudetica	126	77 (61%)

7.22 Types of damage and the predators

The data in Table 7.22-1 show that seed predation and capsule predation occurred on plants of all five species of Pedicularis at both the McConnell River and Churchill. Since data were available for only two species at the McConnell River in 1968, the data for that year were not included in Table 7.22-1, nor in the analyses based on the data in Table 7.22-1. However, the data from 1968 were included in estimates of the overall frequencies of the two types of predation.

Despite small sample sizes, significant differences were detected in the relative proportions of seed and capsule predation at three levels of comparison: (1)

Table 7.22-1. The frequency of seed (Se) and capsule (Cap) predation in marked plants of Pedicularis.[1].

LOCATION	YEAR	PEDICULARIS FLAMMEA Se	PEDICULARIS FLAMMEA Cap	PEDICULARIS LABRADORICA Se	PEDICULARIS LABRADORICA Cap	PEDICULARIS LAPPONICA Se	PEDICULARIS LAPPONICA Cap	PEDICULARIS PARVIFLORA Se	PEDICULARIS PARVIFLORA Cap	PEDICULARIS SUDETICA Se	PEDICULARIS SUDETICA Cap
McConnell	1965	2	11 (15%[2].)	1	3 (25%)	3	4 (43%)	8	10 (100%)	15	3 (83%)
	1966	(13	8) (62%)	25	11 (69%)	(8	16) (33%)	(41	6) (87%)	40	10 (80%)
	1967	--		1	0 (100%)	0	3 (0%)	3	0 (100%)	9	0 (100%)
Churchill	1966	8	9 (47%)	6	10 (37%)	1	7 (13%)	--		0	23 (0%)
	1967	2	5 (29%)	1	3 (25%)	0	1 (0%)	--		1	6 (14%)

1. The data from sites are pooled within years; parentheses indicate years with significant differences between sites (see Table 7.22-2).
2. The percentage of seed-predated attempts out of the total damaged attempts per year.

between sites for three species in 1966 at the McConnell River (Table 7.22-2), (2) between locations in Pedicularis sudetica, in both 1966 and 1967 (Table 7.22-3) and (3) between some species in 1965 and in 1967 (Table 7.22-3). Data which included significant differences between species were not used in the tests between years or species. The overall proportion of seed predation observed in damaged reproductive attempts (1965-1967) varied among species from 32% in Pedicularis lapponica to 90% in P. parviflora (Table 7.22-4).

(a) seed predators

Insects, the only predators which fed inside ovaries and capsules, were detected by (1) the presence of larva(e) or feces inside the ovaries and capsules, (2) scars in the calyx and in the wall of the ovary or capsule made by ovipositing insects (see Neff 1968) and (3) the presence of puparia with the collections of fruit. Observations in Table 7.22-5 illustrate the variability in the number of capsules occupied by insect larva(e) and in the total seed output among seed-predated plants of Pedicularis flammea.

The seed predators most commonly found, based on a total of at least 100 larvae and puparia (per genus) from the capsules of marked plants, were species of flies (Diptera) in the genera Phytomyza and Gimnomera (Table 7.22-6). Only the genera of these flies are listed in Table 7.22-6 because sufficient specimens of adult flies

Table 7.22-2. Significant differences between sites (within years) in the relative proportions of seed (Se) and capsule (Cap) predation.[1].

PEDICULARIS FLAMMEA				PEDICULARIS LAPPONICA				PEDICULARIS PARVIFLORA			
SITE	Se	Cap		SITE	Se	Cap		SITE	Se	Cap	
3	5	1	*	1	4	0	*	6	4	4	*
5	3	0	*	5	0	8		10	12	0	
11	1	7									

1. McConnell River, 1966; 2 X 2 tests (exact probability).

Table 7.22-3. A summary of the significant differences in the relative proportions of seed and capsule predation.[1].

COMPARISONS		SIGNIFICANT DIFFERENCES
Within species		
Between years		None
Between locations		Pedicularis sudetica 1966 McConnell and Churchill **
		1967 McConnell and Churchill **
Between species		
McConnell	1965	P. flammea and P. sudetica**
		P. flammea and P. parviflora**
		P. lapponica and P. parviflora*
		P. labradorica and P. parviflora*
	1967	P. lapponica and P. sudetica*
Churchill	1966	P. flammea and P. sudetica**
		P. labradorica and P. sudetica**

1. 2 X 2 tests. Tests between years, locations and species were not conducted using data from years in which there were significant differences between sites (Table 7.22-2).

Table 7.22-4. The overall frequency of seed predation and capsule predation in damaged reproductive attempts (1965-1968) at the McConnell River.

PEDICULARIS	TOTAL DAMAGED ATTEMPTS	SEED-PREDATED ATTEMPTS	CAPSULE-PREDATED ATTEMPTS
lapponica	34	11 (32%)[1]	23
flammea	38	16 (42%)	22
labradorica	41	27 (66%)	14
sudetica	77	64 (83%)	13
parviflora	58	52 (90%)	6

1. The percentage of seed-predated attempts out of the total damaged attempts is shown in parentheses.

Table 7.22-5. Observations on seed-predated plants of Pedicularis flammea at the McConnell River (19 August, 1968).

OBSERVATIONS	PLANTS				
	1	2	3	4	5
Number of capsules per plant	11	10	5	5	5
Number of capsules occupied by insect larva(e)	1	4	3	2	4
Number of larva(e) per capsule	1	2, 3 2, 2	3, 5 3	2, 2	3, 2 4, 3
Number of seeds remaining in occupied capsules when examined	12	0, 0 0, 0	0, 0 0	0, 5	0, 0 0, 0
Total number of seeds per plant	151	135	36	75	16

Table 7.22-6. Insects found feeding on ovaries, ovules, and developing seeds of Pedicularis at the McConnell River (1965-1968).

INSECTS	PEDICULARIS	LOCATIONS OF LARVAE
Phytomyza spp. (Diptera: Agromyzidae)	all species[1].	in ovaries and capsules
Gimnomera spp. (Diptera: Scatophagidae)	flammea sudetica	in ovaries and capsules
Gonarcticus sp. (Diptera: Scatophagidae)	flammea	in the corolla tube, in ovaries, in stem and caudex.

1. Also from Pedicularis labradorica, Churchill.

of both sexes are not yet available for identification of the species. Thus it is not known whether one or more species of Phytomyza and of Gimnomera are associated with all or only some of the species of Pedicularis.

Twenty-two larvae in a third genus of flies (Gonarcticus) were found inside ovaries feeding on ovules and inside corolla tubes feeding on ovaries in young inflorescences of Pedicularis flammea during examinations of the flowers in 1968. These flies have also been considered seed predators (as well as capsule predators) of Pedicularis flammea at the McConnell River (Table 7.22-6) although they were not detected in the collections of capsules of the reproductive survey. In older plants of P. flammea

(i.e. plants with capsules) the larvae of these flies were found inside the stems and caudices (modified hypocotyl region of stems) rather than in the capsules. Thus, larvae of Gonarcticus could have been present in the marked plants but they would not have been detected in the collections of capsules. Similarly, other seed predators may not have been detected in this limited survey because they were not in the capsules when the capsules were harvested.

Flies in the genera Phytomyza, Gimnomera, and Gonarcticus have also been found with species of Pedicularis in other parts of North America, in Europe, and in Greenland (Phytomyza spp., Hering 1949, Rydén 1956, Griffiths 1968, Spencer 1969; Gimnomera spp. Rydén 1956, Neff 1968, Vockeroth personal communication; Gonarcticus spp. Vockeroth 1958, and personal communication). Some examples of Diptera-Pedicularis associations noted by other authors are summarized in Table 7.22-7.

Neff's (1968) studies on the biology of Gimnomera cerea provide details on the Gimnomera-Pedicularis canadensis relationship which might be applicable to the Gimnomera spp. - Pedicularis sudetica and P. flammea relationships (Table 7.22-6). For example, Neff found that a female fly oviposits directly into an ovary and that the larva(e) remain(s) inside the ovary-capsule until ready to exit for pupation. Thus, if the larva does not move from ovary to ovary, the ovule and seed damage to the plant would depend on the amount of feeding done by each larva inside a

Table 7.22-7. Examples of Diptera - *Pedicularis* associations reported in the literature.

DIPTERA	PEDICULARIS	COMMENTS ON BIOLOGY
Phytomyza		
pedicularicaulis	*canadensis*	adult flies on the inflorescences or stems; larvae feed in stems (Spencer 1969)
pedicularidis	*groenlandica*	adults on flowers; puparia in seeds (Spencer 1969)
tenella	*palustris*	larvae inside seeds in capsules, pupate in soil (Griffiths 1968)
affinis	*canadensis*	larvae feed in capsules, pupate externally (Griffiths 1968, Spencer 1969)
diversicornis	*palustris*	larvae from stems (Hering 1949)
nigroorbitalis	*lapponica*	adults caught from flowers (Lappland); larvae live in fruit (Rydén 1956)
Gimnomera cerea	*canadensis*	female oviposits into the ovary of a flower; eggs hatch in 3-5 days; larvae feed on ovules and capsule, leave dehisced capsule (or make exit slits), pupate 3-5 cm below the soil surface (Neff 1968).

developing capsule and the proportion of ovaries and capsules occupied by larva(e). The proportions of ovaries and capsules occupied by larvae would be expected to depend on such factors as the number of ovipositing females, the number of "suitable" buds, flowers, or capsules for ovipositing, the quantity of eggs laid and their distribution (e.g. several eggs per ovary, one or more eggs in each of several ovaries, eggs laid on one or several inflorescences), and the survival of the eggs and larvae.

Neff (1968) observed that females of Gimnomera cerea oviposited in up to 15 or 20 flowers per inflorescence of Pedicularis canadensis, selecting only flowers in full bloom. Thus, if similar egg laying behavior occurred in Gimnomera spp. at the McConnell River, a single female could deposit eggs in all the ovaries of an average plant of Pedicularis flammea (mean = 7 flowers) or in about half the ovaries of an average plant of P. sudetica (mean = 48 flowers), assuming that all the flowers were suitably developed.

(b) capsule predators

At the McConnell River, the only animals which I have observed removing flowers from an inflorescence or removing entire inflorescences from plants of Pedicularis were blue geese (Chen caerulescens) and Canada geese (Branta canadensis). Although these observations did not include the marked plants of the reproductive survey, geese have clearly fed within the survey sites and undoubtedly

contributed to the destruction of ovaries and capsules, whether or not they actually ate the flowers or inflorescences. Fly larvae in the genus Gonarcticus have been observed eating ovaries in young flowers of Pedicularis flammea at the McConnell River; therefore, they were also classed as capsule predators.

Other herbivores, present in and around the study area, which may also be capsule predators include the following: voles (Microtus sp., Clethrionomys sp.), lemmings (Lemmus trimucronatus, Dicrostonyx torquatus), Parry's ground squirrel (Citellus parryii), arctic hare (Lepus arcticus), and barren ground caribou (Rangifer tarandus groenlandicus). Hares (Kevan 1970), caribou, or reindeer (Cody 1965, Kelsall 1968), and muskoxen (Brassard and Beschel 1968) have been observed feeding on inflorescences of species of Pedicularis in other parts of northern Canada.

7.23 Predation and seed output

The most extreme effect of predation on the seed production of a given reproductive attempt would be reproductive failure. Table 7.23-1 shows that reproductive failures occurred in 12% (Pedicularis parviflora) to 65% (P. lapponica) of the damaged plants. As with the incomplete reproducers, the reproductive failures of damaged plants also contributed to a reduction in reproductive efficiency. Pedicularis parviflora, the species which had the highest reproductive efficiency, also had the fewest reproductive failures due to predation.

Table 7.23-1. The frequency of reproductive failures due to seed and capsule predation in Pedicularis at the McConnell River (1965-1968).[1].

PEDICULARIS	DAMAGED ATTEMPTS	NUMBER OF REPRODUCTIVE ATTEMPTS FAILURES	FAILURES DUE TO: SEED PREDATION	FAILURES DUE TO: CAPSULE PREDATION
parviflora	58	7 (12%)	3	4 (57%)
labradorica	41	7 (17%)	1	6 (86%)
sudetica	77	17 (22%)	9	8 (47%)
flammea	38	13 (34%)	2	11 (85%)
lapponica	34	22 (65%)	0	22 (100%)

1. Percentages indicate the percentage of damaged attempts which were failures and the percentage of failures due to capsule predation.

The inflorescences (and potential capsules) of capsule-predated plants disappeared before the end of floral anthesis in all plants, except for three of Pedicularis flammea. The high percentage (65%) of reproductive failures among damaged plants of Pedicularis lapponica, all due to capsule predation, may be partly a reflection of the ease with which an animal can remove the whole inflorescence. The inflorescences of Pedicularis lapponica have few flowers per stem (usually less than eight) and the buds and flowers are relatively tightly clustered before and during anthesis. Although inflorescences of Pedicularis flammea have few

flowers per stem and inflorescences of P. labradorica may have few flowers on an unbranched stem, the flowers usually are not all clustered at the top. Thus, one or two flowers may remain near the base after the top of the stem has been removed. Similarly, the size and structure of plants of P. parviflora and P. sudetica (i.e. branched or multiple inflorescences) may have contributed to the low frequency of reproductive failures observed among damaged attempts.

Seed predated plants completely lacked seeds in a total of 15 reproductive attempts (Table 7.23-1). These failures occurred in Pedicularis flammea, P. parviflora, and P. labradorica in 1966 and in all years with data (1965, 1966, 1967) in P. sudetica. The failures corresponded with years of relatively high frequencies of plants with seed predation (Table 7.22-1). Unfortunately the condition of each capsule was not recorded: such information would have shown whether all the capsules had in fact been occupied by larva(e).

Comparisons between the seed outputs of damaged and undamaged reproductive attempts were made among the plants within a site using a nonparametric Mann-Whitney U-test (Table 2.4-1). A nonparametric test was used because the data from damaged plants consisted entirely of zeros in one site, and it was apparent from the original data of other sites that the frequency distributions of the number of seeds in damaged plants would often be skewed (see original data in Tables A6.1-1 to A6.1-5). Sites with very

small samples (less than three damaged plants or less than three undamaged plants) were not included in these comparisons of seed output.

Table 7.23-2 summarizes only the data from sites in which significant differences in seed output were found between damaged and undamaged plants. Only one comparison was possible for Pedicularis flammea because of the small sample sizes and the high proportions of either damaged or undamaged plants per site. In the one test which was possible (Site A2, 1965), seed output differed at the 10% level but not at the 5% level (the mean number of seeds in three damaged plants was 22; in seven undamaged plants, 115). When the pooled mean seed output for undamaged and damaged plants was examined in this species (Table 7.23-3), the mean number of seeds in undamaged plants was 102.4 whereas the mean number of seeds in damaged plants was 27.7. This difference suggests that if sample sizes had been adequate, significant differences in seed output would probably have been detected between damaged and undamaged plants of Pedicularis flammea.

No differences in the seed output of damaged and undamaged plants were found in Pedicularis sudetica (Table 7.23-2). The pooled mean numbers of seeds per undamaged plant and per damaged plant were 38.8 and 33.5, respectively (Table 7.23-3). However, in two sites for P. labradorica and in three sites for P. lapponica, the damaged plants had significantly fewer seeds than the

Table 7.23-2. A summary of significant differences in seed output between damaged and undamaged plants (within a site) at the McConnell River.[1].

PEDICULARIS	CLASS	COMPARISONS OF THE NUMBER OF SEEDS PER PLANT[2].								
flammea		(1 test)[2].								
labradorica		(6 tests)								
		Site A2, 1965			Site 2, 1966					
		n	Mean	U	n	Mean	U			
	damaged	3	10.7	*	8	20.1	**			
	undamaged	7	64.1		9	61.4				
lapponica		(6 tests)								
		Site A3, 1965			Site 3, 1966			Site 5, 1966		
		n	Mean	U	n	Mean	U	n	Mean	U
	damaged	5	0.6	*	6	0.7	*	8	0.0	**
	undamaged	3	24.0		8	4.0		9	10.0	
parviflora		(7 tests)								
		Site A5, 1965			Site 4, 1966			Site 7, 1966		
		n	Mean	U	n	Mean	U	n	Mean	U
	damaged	6	283.3	*	9	290.4	*	9	150.7	**
	undamaged	13	116.9		11	135.2		11	30.4	
sudetica		(6 tests)								

1. Mann-Whitney U-test (Table 2.4-1). n = the number of damaged, or undamaged, plants within a site.
2. The number of possible tests for a species is indicated in parentheses (see text).

Table 7.23-3. Pooled mean seed output in damaged and undamaged plants of Pedicularis at the McConnell River (1965-1968).

	MEAN SEED OUTPUT PER REPRODUCTIVE ATTEMPT			
	UNDAMAGED PLANTS		DAMAGED PLANTS	
PEDICULARIS	NUMBER OF PLANTS	MEAN	NUMBER OF PLANTS	MEAN
flammea	38	102.4	36	27.7
lapponica	98	11.2	34	3.6
labradorica	75	52.5	41	47.1
sudetica	49	38.8	77	33.5
parviflora	80	122.5	58	222.9

undamaged plants. The same trend is apparent from the pooled mean seed output for these two species (Table 7.23-3). In contrast, the damaged plants of Pedicularis parviflora had significantly more seeds than the undamaged ones (Table 7.23-2) in three out of seven possible tests. Furthermore, in Pedicularis parviflora the overall mean seed output for damaged plants was 100 seeds per plant higher than for undamaged plants.

The similarity in the numbers of seeds of undamaged and damaged plants may indicate such conditions as: (1) very little damage (i.e. only a few flowers missing, or a few capsules inhabited by larvae), (2) compensation for removal of reproductive parts by the development of

additional buds, capsules or ovules (McAlister and Krober 1957, Hicks and Pendleton 1969), (3) selection of larger plants (i.e. ones with more flowers) by predators, or (4) a combination of these. In Pedicularis parviflora, the damaged plants in Sites A5, 4 and 7 which had significantly more seeds than undamaged plants also had significantly more capsules per plant than undamaged plants (Table 7.23-4). Since insects were responsible for the damage in 22 out of 24 of these damaged plants (see Table A7.22-1), the results suggest that adult flies select larger plants for oviposition. However, factors other than size may also have influenced the apparent "selection" of plants by insects. For example, larger plants might flower earlier than smaller ones and therefore be more available, as a group, to ovipositing flies than small plants.

The contribution of seed and capsule predation to reproductive failure and, in some cases, to reduced reproductive efficiency represents one of the more striking findings in this study since the challenges to seed production in the arctic have usually been attributed to physical (i.e. low temperatures) rather than biotic factors (Porsild 1951a, Bliss 1962, Savile 1966, 1972, Billings and Mooney 1968). The importance of seed and fruit predation on seed mortality and on the evolution of plants has only recently been appreciated in tropical and temperate ecosystems (Huffaker 1959, Harris 1963, DeBach 1964, Janzen 1969, 1970, Cantlon 1969). The information here documents

Table 7.23-4. Comparisons of the number of capsules between damaged and undamaged plants of Pedicularis parviflora in three sites at the McConnell River.

SITE / YEAR	CLASS	NUMBER OF PLANTS	CAPSULES PER PLANT RANGE	MEAN	U[1].	
A5 / 1965	damaged[2].	6	33 - 112	78.0		*
	undamaged	13	1 - 141	31.8		
4 / 1966	damaged[2].	9	17 - 184	82.1		*
	undamaged	11	7 - 111	43.3		
7 / 1966	damaged[3].	9	7 - 131	36.7		**
	undamaged	11	2 - 23	9.5		

1. Mann-Whitney U-test (Table 2.4-1).
2. Includes only seed-predated plants.
3. Includes seven seed-predated plants, two capsule-predated plants.

the existence of plant and seed predator interactions in an arctic ecosystem.

Further studies of insects associated with the species of Pedicularis at the McConnell River could reveal what appear to be relatively complex interactions between plants and insects, as well as increase the number of insect species known for the area (insects collected from Pedicularis in 1968 probably include at least five new species). Both types of information would add significantly to our understanding of species diversity and of interactions

between species in an arctic ecosystem (cf. Downes 1964, Dunbar 1968).

Chapter 8

POLLINATION AND SEED PRODUCTION

The purposes of this phase of the research were to determine whether seed-set occurred when insects were prevented from visiting the flowers of Pedicularis and to observe whether there were visitors to the flowers which were likely to be pollen vectors. These preliminary studies also provide some clues about the breeding systems of the species of Pedicularis at the McConnell River: without assistance it was impractical to attempt more extensive field studies of pollination and fertilization.

An assumption made in this study is that seed production in the species of Pedicularis at the McConnell River and at Churchill involves sexual reproduction (see Appendix C). If seeds are produced in flowers isolated from insects, they are tentatively assumed to have been produced as a result of self-fertilization.

The flowers of the five species at the McConnell River were described in Section 4.2.

8.1 Insect exclusion and seed production

The following methods were used to exclude insects from the flowers of Pedicularis. Small parchment bags, commonly used in genetic studies (Filion 1970) and readily

cut into various lengths (No. 317 shoot bags, 8 x 19 cm, from Corn States Hybrid Service,Inc., Des Moines, Iowa), were placed over young inflorescences before floral anthesis in Pedicularis flammea and before the protrusion of the stigma from unopened buds in the other four species. The length of the bag was adjusted, depending on the species, to allow space for stem and rachis elongation; the bags were enclosed securely around stems with paper covered wires; and the bags, plus stems, were left free to move in the wind. The bags were left on the inflorescences until the plants were harvested for examination. Only the flowers on the main stem were bagged in Pedicularis parviflora and P. labradorica.

Insect exclusion experiments were conducted at the McConnell River in 1966 through 1968. Each year, potentially reproductive plants of each species around randomly selected points were numbered (using numbered garden tags placed adjacent to the plants), then allocated randomly to either bagged or control treatments. All plants of one species were marked in one site; areas adjacent to the first site were used in subsequent years. The main axis for sampling was a line between poles 04 and 14 of the permanent grid of the study area (Figure B-1): points for the sample sites were located within 500 m of this axis.

In 1966 and 1967, the treatments initially consisted of 50 control plants and 50 bagged plants per species, with the following exceptions: (1) there were no bagged plants of Pedicularis flammea in 1966, (2) there were only 13 bagged

plants of P. parviflora in 1966 and (3) there were 53 control plants of P. sudetica in 1967. In 1968, the treatments consisted of 12 or 14 bagged plants per species and 20 control plants per species. In addition, 50 inflorescences of Pedicularis lapponica were bagged at Churchill in 1966 in the reproductive survey sites 1 and 2. Sampling was conducted so that the marked plants for the reproductive survey could be used as controls in each site.

In some cases over half of the bagged and the control inflorescences disappeared or were damaged before harvest (both locations). Therefore, the sample size reported hereafter refers only to the inflorescences which could be recovered intact.

In this study, the entire plant, or the bagged part of the plant, rather than an individual flower or capsule, was scored for the presence or absence of seeds. Plants were harvested for scoring as soon as dehiscing fruits were observed on the control plants (1966, 1967).

In 1968, the numbers of seeds per capsule were also determined. Therefore the inflorescences of Pedicularis flammea, P. labradorica and P. lapponica were collected just before seeds would normally be released from the control plants, judged by the date when the first dehisced capsule of each species was found in the study area. Since no capsules of P. sudetica and P. parviflora had dehisced by the end of the field period in 1968, inflorescences of these species were collected on 20 August and only the presence or

absence of nearly mature seeds (i.e. seeds of approximately normal size) was recorded per inflorescence.

The final sample sizes and the numbers of bagged and control plants with seeds are listed for each year in Table A8.1-1. Since there were no significant differences (2 X 2 tests, exact probability, $P>0.05$) between years in the frequency of bagged and control plants with seeds within four species (Pedicularis flammea, P. lapponica, P. parviflora and P. sudetica), the data for each of these species were pooled for tests between treatments (Table 8.1-1).

In Pedicularis flammea, there was no significant difference in the frequency of bagged and control plants with seeds (Table 8.1-1). The data on seeds per capsule show that there was also no significant difference between the mean number of seeds in bagged capsules and control capsules of P. flammea (Table 8.1-2, original data in Table A8.1-2). The mean values compared here (Table 8.1-2) were the mean number of seeds per capsule (per plant) since the variances were heterogeneous among the plants of the two treatments on count, square root, and logarithmic scales (Table A8.1-3).

These results suggest that neither the exclusion of flower visitors, nor the actual technique of bagging plants, had a significant effect on the average quantity of seeds produced by this species. Thus, there was no implication that an absence of pollinators would have a negative effect

Table 8.1-1. The numbers of bagged and control plants of *Pedicularis* with seeds (McConnell River).[1.]

PEDICULARIS	YEARS TESTED	TREATMENT	NUMBER OF PLANTS TOTAL	WITH SEEDS	2 X 2 TESTS (CHI SQUARE)
flammea	1967,1968	control	38	36	0 ns
		bagged	46	46	
parviflora	1966-1968	control	79	79	60.5 **
		bagged	47	19	
sudetica	1966-1968	control	121	106	108.1 **
		bagged	86	13	
lapponica	1966-1968	control	84	80	159.6 **
		bagged	91	0	

1. Data for *Pedicularis labradorica* was not pooled (see text).

Table 8.1-2. Comparison of the number of seeds per capsule in bagged and control plants of *Pedicularis flammea* (McConnell River, 1968).[1.]

	BAGGED PLANTS	CONTROL PLANTS
Number of plants	12	19
Mean number of seeds per capsule (per plant)	20.4	17.5
Variance	15.3	44.0

F = 2.88 * t' = 1.56 ns

1. Based on the mean number of seeds per capsule, per plant.

on the seed output of individual plants or on the reproductive efficiency of the species. As seen in Table 8.1-2, the capsules of bagged inflorescences actually averaged slightly more seeds per capsule than the control plants.

Table 8.1-2 also shows that there was a significant difference in variance between bagged and control treatments. Observations suggested that the high variability among the control plants might be related more to seed predation than to pollination and fertilization. In the original data in Table A8.1-2, it can be seen that eight of the control plants averaged fewer seeds per capsule than any of the bagged plants. Five of these eight control plants contained insect larvae in the capsules: for example, the two plants which averaged 3.2 seeds and 7.2 seeds had Dipteran larvae in four out of five capsules, and three out of five capsules, respectively. None of the bagged capsules contained insect larvae. If all of the seed-predated capsules are removed from the observations, the overall mean number of seeds per capsule in controls becomes 19.3 seeds, reducing the difference between treatments to 1.1 seeds per capsule. Thus, the bagging of inflorescences can be somewhat beneficial to seed production in Pedicularis flammea, primarily by preventing seed predation.

In contrast to Pedicularis flammea, none of the bagged plants of Pedicularis lapponica at the McConnell River produced any seeds (Table 8.1-1). Similar results were obtained at Churchill (1966): 26 bagged plants lacked seeds,

25 control plants possessed seeds. These results imply that an absence of pollinators could have a large negative effect on the seed output of individual plants and on the reproductive efficiency of the species.

The control plants of P. lapponica at the McConnell River in 1968 had an average of 3.9 seeds per capsule (Table A8.1-4); they clearly differed from the bagged plants with no seeds per capsule. Since the inflorescences of P. flammea produced abundant seeds in bags in concurrent tests, it seems that the bagging itself was unlikely to have had such a drastic negative effect on seed production in P. lapponica but not in P. flammea. Two of the control plants also completely lacked seeds (Table A8.1-3), indicating that conditions resulting in the absence of seeds were not associated with bagged plants only.

In the remaining three species of Pedicularis some of the bagged plants produced seeds and others did not (Tables 8.1-1 and 8.1-3). The proportions of bagged plants with seeds were consistent among years in Pedicularis parviflora and P. sudetica and there were significantly fewer bagged plants than control plants with seeds (Table 8.1-1). In Pedicularis labradorica, the results were more complex: in 1966 and 1968 there were no differences between treatments, most plants possessed seeds; in 1967 there were significantly fewer bagged plants than control plants with seeds (Table 8.1-3). On the basis of the examination of

Table 8.1-3. The numbers of bagged and control plants of Pedicularis labradorica with seeds (McConnell River).[1]

YEAR	TREATMENT	TOTAL NUMBER OF PLANTS	NUMBER OF PLANTS WITH SEEDS
1966	control	50	50
	bagged	30	29 b
1967	control	24	21 a
	bagged	26	11 a b
1968	control	19	19
	bagged	5	4

1. Data followed by the same letter are significantly different (2 X 2 tests, exact probability, $P<0.01$).

seeds per capsule in the bagged plants of P. labradorica, which will be discussed in subsequent paragraphs, and the uniformity of the methods used in the field, it appears that the presence or absence of seeds on bagged plants is due to differences among the plants (perhaps genetical or morphological) rather than experimental technique. The results for these three species thus suggest that a lack of pollinators could have a negative effect on the seed output of some individual plants, at least in some years, and on the reproductive efficiencies of these species.

The variation between years and treatments in the frequency of plants of Pedicularis labradorica with seeds is shown in Table 8.1-3. A significant difference in the frequency of bagged plants with seeds was detected in 1966

and 1967 (97% of the bagged plants possessed seeds in 1966; 42%, in 1967). No significant difference was detected in the frequency of control plants with seeds for the same years. Although 80% (4 out of 5) of the bagged plants in 1968 possessed seeds, the sample size in 1968 was sufficiently small that a statistically significant difference from the 1967 data was not detected.

In 1968, when seeds per capsule were determined in Pedicularis labradorica, no difference in the mean number of seeds per capsule was detected between treatments (Table 8.1-4). A difference might have been detected, however, if similar comparisons had been made in 1967 when a lower proportion of the bagged plants produced seeds (Table 8.1-3).

In contrast to Pedicularis flammea, the bagged plants of P. labradorica showed greater variability among plants than the control plants (Table 8.1-4). For example, the mean number of seeds in the five bagged plants ranged from 0.0 to 13.3; in the 19 control plants, from 4.9 to 12.8 (Table A8.1-5). Thus, the average number of seeds per capsule produced in the five bagged plants ranged from less than to slightly greater than the average number found in the controls. Since some of the bagged plants had few or no seeds and some had numerous seeds, it was deduced that the variability in seed production between individual bagged plants was due to different characteristics of the plants.

One probable reason for the failure of seed production in all, or some, of the bagged plants of Pedicularis lapponica,

Table 8.1-4. Comparison of the number of seeds per capsule in bagged and control plants of Pedicularis labradorica (McConnell River, 1968).[1]

	BAGGED PLANTS	CONTROL PLANTS
Number of plants	5	19
Mean number of seeds per capsule (per plant)	6.6	8.6
Variance	39.9	4.5

F = 8.96 *** t' = 0.73 ns

1. Based on the mean number of seeds per capsule, per plant.

P. labradorica, P. parviflora, and P. sudetica is the lack of self-fertilization. Hence, experiments are needed to determine whether all or some of the plants of these species at the McConnell River are self-incompatible. Since there is little evidence for self-fertility in the genus Pedicularis (Sprague 1960, Macior 1970) and no evidence of self-fertility in insect-isolated inflorescences of Pedicularis sudetica in Colorado (Macior 1970), self-sterility is a plausible reason for seed failure in these species, although not one normally suggested for plants in the arctic (Mosquin 1966). Another plausible reason for seed failure in the bagged plants is lack of pollination. The stigma of the flower in all four of these species is normally separated from the anthers (Table 4.2-1); however, the separation apparently

has not prevented self-pollination in some of the bagged plants of three species. Differences among plants in the timing of stigma receptivity could also account for the presence, or absence, of seeds in the bagged plants.

The variation between years in the proportion of bagged plants of Pedicularis labradorica with seeds may have been due to different frequencies of plants capable of self-pollination or self-fertilization. These frequency differences could occur relatively easily in a predominantly monocarpic population if in some previous year reproductive success was restricted to plants with the tendency to self-pollinate and self-fertilize, especially if factors with a genetic basis were involved. Examples of such factors are the time of stigma receptivity (Moore and Lewis 1965), herkogamy and time of anther dehiscence (Breese 1959), and the degree of self-fertility (Antonovics 1968).

The results obtained at the McConnell River showing that seeds were produced by plants of Pedicularis flammea, P. labradorica, P. parviflora and P. sudetica from which pollinators were excluded are among the first experimental evidence of the production of seeds independently of pollen vectors in species of Pedicularis in North America (cf. Macior 1970). Kevan (1970) has also found that seeds were produced on plants of Pedicularis arctica in insect-excluding cones on Ellesmere Island, N.W.T., Canada. On the other hand, the implication that all, or some, plants of four species of Pedicularis might require pollen vectors for seed production

is interesting because such a strategy is generally considered risky in an arctic environment where the number and abundance of species of possible pollen vectors are low and their activities are often negatively affected by severe weather.

8.2 Insect visitors and pollinators

In 1968 observations of flowers and flower visitors were made at various times between 0400 and 2400 hours during the flowering periods of the species of Pedicularis at the McConnell River. If no flower visitors were observed in 30 to 60 minutes, the observations were abandoned and resumed at another time. A minimum of 15 hours was spent watching flowers of each species of Pedicularis in areas with a single species (P. sudetica only) and in areas with several species together. Because insect visitors to the flowers of Pedicularis sudetica were relatively numerous, an additional 20 hours was spent observing and photographing its visitors. The total period of observation was 111 hours: this represented 12% of the total number of hours available from the date of first flowering of plants of Pedicularis (15 July) until the completion of field work on 21 August (38 days x 24 hours). All visitors to the flowers were recorded.

I noted the approach of insects to flowers, the insect's orientation on the flower, the position of the anthers and stigma with respect to the insect, and whether

flowers of other plants of the same species or other species of Pedicularis were visited. Insect specimens were collected and examined for the presence of pollen of Pedicularis on the body (e.g. in the corbiculae of the hind legs of bumblebees). Pollen was mounted in lactophenol and identified as Pedicularis (genus only, see Appendix D) or foreign (non-Pedicularis).

From the field observations, the following criteria were selected to identify the flower visitors that were most likely to be pollen vectors: (1) rapid visits to more than one flower, (2) visits causing the release of pollen onto the body, and (3) making contact with the stigma on the same parts of the body that received pollen. Other insects visiting a flower but not completing all of these activities might sometimes transport pollen; however, they were not classed as pollen vectors in this study (cf. Faegri and van der Pijl 1966).

I also watched bumblebees to determine the periods during which they were active and which species of flowers they visited at the McConnell River, because bumblebees have frequently been cited as flower visitors, or, the only probable pollinators of species of Pedicularis in other subarctic and arctic areas (Aurivillius 1883, Mathiesen 1921, Ekstam cited in Høeg 1924, O. W. Richards 1927, Lagerberg et al. 1957, Anderson 1959, Savile 1959, Shamurin 1966, Hocking 1968, Kevan 1970, K. W. Richards 1970 and personal communication).

Insects collected from the flowers of Pedicularis were identified by scientists of the Entomology Research Institute, Canada Department of Agriculture, Ottawa: R. de Ruette (Coleoptera); D. R. Oliver, G. E. Shewell, and J. R. Vockeroth (Diptera); H. E. Milliron (Hymenoptera); and T. N. Freeman (Lepidoptera). Reference specimens were deposited in the Canadian National Collection (CNC), Ottawa.

Figure 8.2-1 shows the periods of flowering of the five species of Pedicularis in 1968 and the number of hours that I spent observing the flowers between 15 July and 21 August (excluding 5 through 7 August when I was absent from the study area). The flowering periods indicate when flowers of a species of Pedicularis would be exposed to pollen vectors; or, when pollen or nectar, or both, would be available as food resources.

Two species of bumblebees were found at the McConnell River (Table 8.2-1). The bumblebees were seen outside the study area on 11 July and inside the study area each day after 15 July except on extremely rainy or windy days (e.g. 29, 30 July; 2, 8, 11, 15 August; Figure 8.2-1). The approximate pattern of development of the bumblebee colonies, as indicated by collected individuals, is given in Table 8.2-1. Since workers of Bombus sylvicola were collected on 26 July, overwintering queens of B. sylvicola were undoubtedly active before 21 July, the date when a queen was first collected in the study area visiting Pedicularis lapponica.

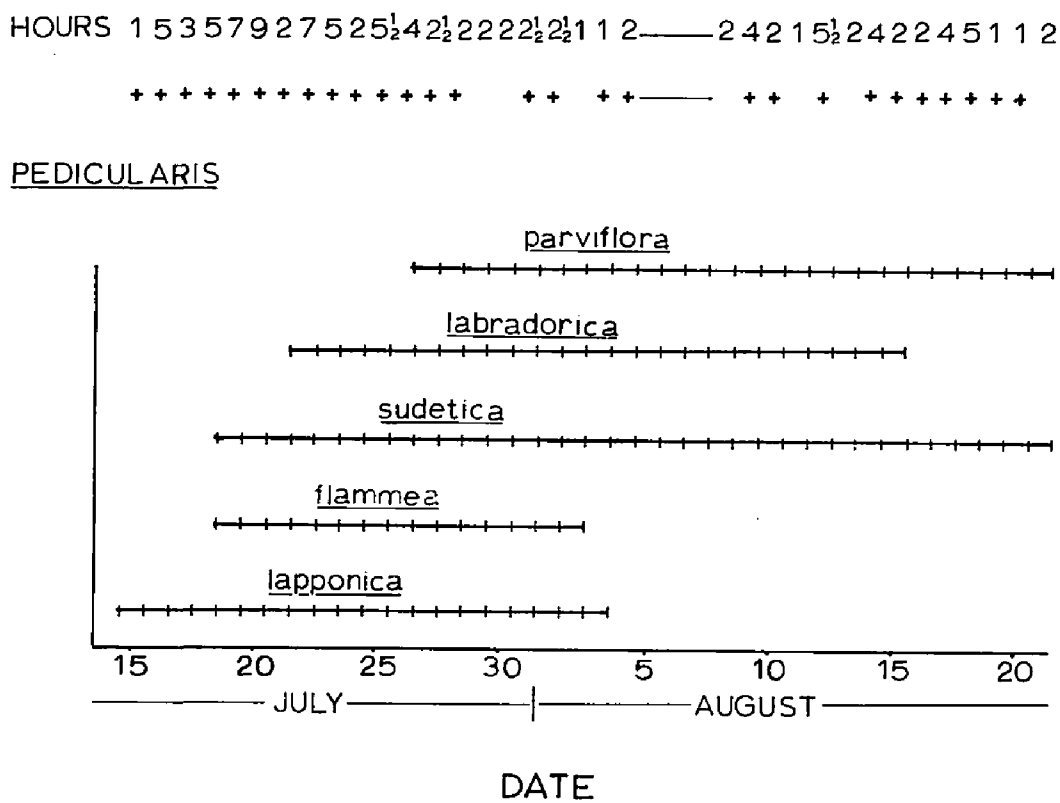

Figure 8.2-1. The flowering periods of Pedicularis, number of hours of observation, and the days when bumblebees were observed (+) at the McConnell River in 1968.

Table 8.2-1. Date of first collection of queens, workers and males of Bombus spp. at the McConnell River in 1968.

BOMBUS	QUEENS[1].	WORKERS	MALES
sylvicola Kirby	21 July	26 July	18 August
polaris Curt.	17 July	3 August	17 August

1. Queens of one or both species were present but were not collected before 17 July.

Tables 8.2-2 and 8.2-3 list the insect visitors collected, the dates of their collection, their number and sex (or caste) and their activities, according to the species of Pedicularis which they visited. A few insects collected from flowers of Pedicularis in other years are also included. The sex or caste is indicated in these tables by the following symbols: F, female; M, male; Q, queen; W, worker; and "?", sex not reported. The activities of the flower visitor are signified by these categories:

R: insect rested, without moving, on the flower or the inflorescence

N: insect faced into or entered the corolla tube; actual or attempted nectar feeding

N/P: insect entered the flower, positioned itself as in N for nectar feeding and disturbed the galea, releasing pollen down onto the dorsal surface of the body (confirmed by microscopic examination of pollen removed from the insect)

C: presence of pollen load in corbiculae of Bombus (followed by the number and caste of bees collected)

Table 8.2-2. Insect visitors to flowers of Pedicularis sudetica based primarily on the specimens collected in 1968 (McConnell River).[1]

INSECT	DATE	NUMBER AND SEX	ACTIVITY
DIPTERA			
Empidae			
Rhamphomyia obscura Zett.	18A	1F	U
Simuliidae			
Schonbaueria furculata (Shew.)	17A	1?	U
Syrphidae			
Helophilus borealis	8A	2M	N/P
Staeg.	9A	4F,7M	N/P
	10A	1F	N/P
	12A	5M	N/P
	14A	1M	N/P
	17A	3F,3M	N/P
	18A	1F,5M	N/P
H. groenlandicus O. Fabricius	9A	1F	N/P
Metasyrphus chillcotti Fluke	9A	1M	N
Scatophagidae			
Okeniella dasyprocta (Loew)	18A	1M	U
Scatophaga furcata (Say)	14A	1F	U
Muscidae			
Helina luteisquama Zett.	4A	1M	U
Lasiops subrostratus Zett.	29J(1967)	1F	U
Spilogona princeps Huck.	4A	1F	U
HYMENOPTERA			
Apidae			
Bombus polaris Curt.	24J(1965)	1Q	N/P
	25J	1Q	N/P
	3A	1W	N/P,C
	9A	2Q,3W	N/P,C(1Q,2W)
	12A	2Q,1W	N/P,C(1W)
	14A	1Q,2W	N/P
	16A	3Q,1W	N/P
	17A	3Q,5W,4M	N/P,C(1W)
	18A	6Q,3W,6M	N/P,C(1W)
	21A	1Q,2M	N/P
B. sylvicola Kirby	26J	1W	N/P,C
	4A	1Q	N/P,C
	18A	1W	N/P,C
LEPIDOPTERA			
Phalaenidae			
Syngrapha parilis Hbn.	18A	1?	R
Pieridae			
Colias hecla Lef.	17A	1?	R
C. palaeno Linn.	14,17,18A	3?	R

1. J = July, A = August; other symbols are explained in text.

Table 8.2-3. Insect visitors to the flowers of four species of Pedicularis based primarily on the specimens collected in 1968 (McConnell River).[1]

PEDICULARIS	INSECT			DATE	NUMBER AND SEX	ACTIVITY
parviflora	COLEOPTERA	Cantharidae	Cantharis sp.	29J(1967)	1?	U
	DIPTERA	Scatopsidae	Rhegmoclema reticulatum Cook	31J	2?	U
				1A	1?	U
				3A	2?	U
		Syrphidae	Helophilus borealis Staeg.	29J(1967)	1F	N/P
				16A	1M	N/P
	HYMENOPTERA	Apidae	Bombus polaris Curt.	17A	1Q	N/P,C
			B. sylvicola Kirby	12A(1965)	1W	N/P,C
lapponica	HYMENOPTERA	Apidae	Bombus polaris Curt.	22J	1Q	N/P,C
			B.sylvicola Kirby	21J	1Q	N/P,C
labradorica	DIPTERA	Chironomidae	Cricotopus sp.	28J	2F	U
			Tanytarsus sp.	28J	1F	U
		Sciaridae	Bradysia sp.	28J	1F	U
		Simuliidae	Cnephia eremites Shew.	31J	1F	U
			Schoenbaueria furculata (Shew.)	25J	1?	U
			S. gigantea Rubtz.	3A(1967)	1M	U
flammea	DIPTERA	Chironomidae	Psectrocladius sp.	31J	1F	U
		Simuliidae	Schonbaueria furculata (Shew.)	31J	2?	U

1. J = July, A = August; other symbols are explained in the text.

U: uncertainty about the activity of the insect; insect moved around the corolla but did not enter the corolla tube; did not disturb the anthers, or touch the stigma; did not visit more than one flower while observed.

The observations on flower visitors are summarized here for each of the five species of Pedicularis.

(a) Pedicularis sudetica

Fifteen species of visitors in three orders of insects were collected from the flowers of Pedicularis sudetica (Table 8.2-2), but only four of these species were collected more than once (a sulfur butterfly, Colias palaeno; a syrphid fly, Helophilus borealis; and two species of bumblebees). Most of the butterflies (Lepidoptera) and flies (Diptera) that were collected only once were merely resting, or, I was uncertain about the nature of their activities. On 14 August, however, one individual of Colias palaeno was observed (not collected) with its tongue extended into the corolla tube of a flower of Pedicularis sudetica, presumably feeding on nectar. The butterfly was only partially standing on the flower and its head, the only part of the body near the stigma, did not come in contact with the stigma.

In contrast, the syrphids and bumblebees rapidly positioned themselves on the lower lip of the corolla, extended their tongues into the corolla tube, usually came in contact with the stigma, received a shower of pollen from the anthers, and moved to another flower. The following

details of visits are given for the two most commonly observed and collected visitors to the flowers of Pedicularis sudetica in 1968.

(1) Helophilus borealis (32 individuals collected)

A fly approached and landed on an inflorescence, and then walked onto the left lobe of the lower lip of a flower (see Figure 8.2-2a). It sometimes extended its tongue into the corolla tube two or three times before or while moving forward into a position where the head was completely inserted into the galea above the entrance of the corolla tube. As it moved forward toward the corolla tube, opening the ventral part of the galea with its head, the remainder of the galea, including the style, was bent downward over the fly and the stigma touched the left dorsal side of the fly's thorax. Dilation of the galea was accompanied by the release of pollen; the pollen dropped onto the left side of the thorax. The heavy accumulation of pollen on the left side of the thorax is seen in Figure 8.2-2b.

As the fly backed out of the left side of the flower the parts of the flower generally returned to their normal positions, although occasionally an anther dropped out of the galea or the style dropped from its normal place. When moving to another flower on the same inflorescence, the flies almost always

(a)

(b)

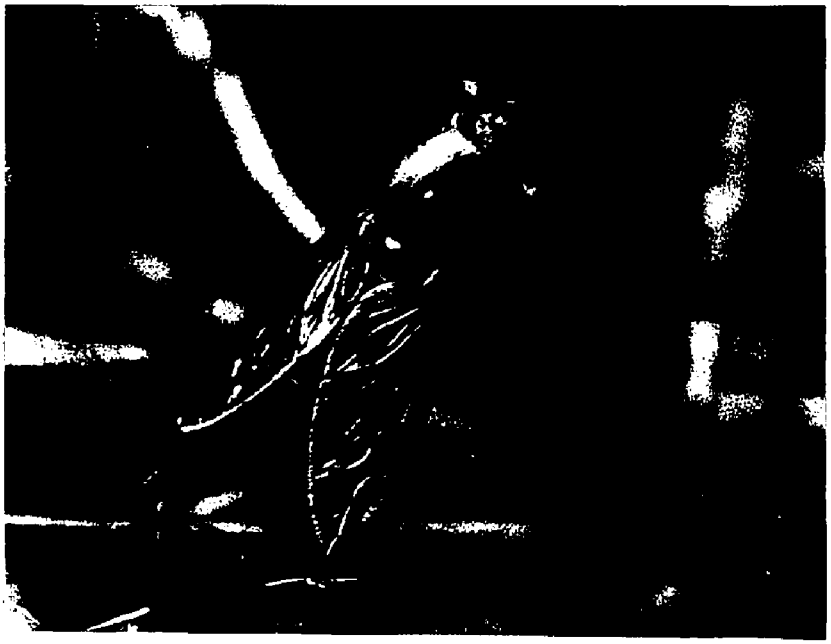

Figure 8.2-2. An individual of Helophilus borealis (a) entering on the left side of a flower of Pedicularis sudetica (X3) and (b) "resting" after visits to Pedicularis sudetica (X4). The arrow indicates the pollen accumulated on the left side of the fly's thorax (b).

(a)

(b)

Figure 8.2-2. An individual of Helophilus borealis (a) entering on the left side of a flower of Pedicularis sudetica (X3) and (b) "resting" after visits to Pedicularis sudetica (X4). The arrow indicates the pollen accumulated on the left side of the fly's thorax (b).

moved in a clockwise direction which coincided with the tilt and deflection of the flowers; thus, the flies entered on the left side of each flower as shown in Figure 8.2-2a.

Five flies, observed from 2 to 3 m, each rapidly visited from 3 to 10 flowers per inflorescence. The flies which remained in the area of observation either flew directly to another plant of Pedicularis sudetica or landed briefly on the ground (for one minute or less), where they remained inactive, or, occasionally wiped their eyes with their fore legs.

The flower visiting of Helophilus groenlandicus, judged from only one fly collected, was similar to that described for H. borealis. When Metasyrphus chillcotti (one fly collected) visited the flowers of one inflorescence, it entered the corolla tube without apparent contact with the stigma or dilation of the galea, undoubtedly because of its small size (approximately one-half as large as Helophilus borealis).

(2) Bombus polaris (48 individuals collected)

Since most (97%) of the bumblebees observed visiting Pedicularis sudetica were individuals of Bombus polaris (Table 8.2-2), the descriptions of bumblebee visits are based on their activities. Unlike individuals of Helophilus borealis which landed directly on an inflorescence, individuals

(especially the queens) of Bombus polaris commonly landed at the base of the stem or on adjacent vegetation and then climbed up the inflorescence, visiting flowers on the way up and around.

Bumblebees generally climbed onto the left lobe of the lip and moved forward, extending the head slightly into the galea and the corolla tube as shown in Figure 8.2-3. When the queens positioned themselves for inbibing nectar, the stigma appeared to touch the dorsal and lateral parts of the queen's head and thorax, and the region between the head and thorax. Bees examined immediately after collection had pollen of Pedicularis on these same parts of the body. The smaller workers and males positioned themselves to imbibe nectar in the same upright manner as the queen. They appeared to have less pollen accumulated on them than the queens, perhaps because they caused less disturbance of the galea and anthers. However, the amount of pollen accumulated on them would also depend on the quantity of pollen present in the flower. The bumblebees visited numerous flowers of an inflorescence but they did not necessarily move in a strictly clockwise direction like the individuals of Helophilus borealis.

Photographic techniques such as those used by Macior (1968a, 1968b, 1969, 1970) are needed to obtain more precise

Figure 8.2-3. A queen of Bombus polaris feeding on nectar in a flower of Pedicularis sudetica. Parts of the flower are illustrated on the left (ll, lower lip; st, stigma; ga, galea, ct, corolla tube). (X4)

Figure 8.2-3. A queen of Bombus polaris feeding on nectar in a flower of Pedicularis sudetica. Parts of the flower are illustrated on the left (ll, lower lip; st, stigma; ga, galea, ct, corolla tube). (X4)

details of stigma and insect contact: Macior was able to document that the stigma in flowers of several species of Pedicularis traversed the crevice between the head and thorax of the bumblebees.

(b) Pedicularis parviflora

Insects were not observed on the flowers of Pedicularis parviflora very frequently and only one insect was actually collected from the flowers more than once in 1968 (Table 8.2-3). This insect was a small Scatopsid fly, Rhegmoclema reticulatum (body less than 2 mm long) which was seen walking on the lower lip of the corolla without touching the stigma or releasing pollen from the anthers (five separate observations). This fly was often found inside the corolla tube in flowers being examined for nectar, which suggests that it was seeking shelter or nectar or both.

The only insects, among those collected in 1968, which touched the stigma and had pollen released onto them were one syrphid (Helophilus borealis) and one queen bumblebee (Bombus polaris). They entered the flowers of P. parviflora in approximately the same manner as described for Pedicularis sudetica. Another syrphid (Helophilus borealis) and a worker bumblebee (Bombus sylvicola) were observed feeding on nectar of Pedicularis parviflora in 1967.

(c) Pedicularis lapponica

Only two queen bumblebees, one of each species, were

observed (and collected) while they were visiting flowers of Pedicularis lapponica in 1968 (Table 8.2-3). The bumblebees entered the flowers on the left side, touched the stigma, and released pollen. On 27 July, another queen of Bombus sylvicola approached inflorescences of P. lapponica twice without landing, then visited flowers of three plants of Astragalus alpinus L. No other insects were seen on the flowers of this species in 1968.

(d) Pedicularis labradorica

Flies from three families were found, and collected once or twice only, on individual flowers of Pedicularis labradorica (Table 8.2-3). All of the flies were small (less than 10 mm in length) and all were seen walking around the lower lip of the corolla.

(e) Pedicularis flammea

The only insects which I found on flowers of Pedicularis flammea (Table 8.2-3) were one midge (Psectrocladius sp.) and two black flies (Schonbaueria furculata). During the observations these insects remained on the lower lip of the corolla only, and did not touch the galea which contained the anthers and stigma.

The insects which were considered probable pollinators of three of the species of Pedicularis at the McConnell River,

based on the observations made primarily in 1968, are summarized in Table 8.2-4. The pollinators included two species of bumblebee which visited three species of Pedicularis, one species of Helophilus which visited two species of Pedicularis, and a second species of Helophilus which visited one species of Pedicularis. No probable pollinators were observed for P. labradorica and P. flammea. Thus, possible pollen vectors were identified at the McConnell River for three out of the four species of Pedicularis (1) which possessed characteristics associated with cross-pollination (see Section 4.2) and (2) which included plants that did not produce seeds in the insect exclusion experiments (Section 8.1).

Although the other visitors to the flowers might have occasionally pollinated some flowers, they seemed to be too small (e.g. Metasyrphus chillcotti) or too long tongued (e.g. Colias palaeno) to release pollen or to touch the stigma. However, if insects such as these feed extensively on nectar, they could reduce the supply of nectar and discourage visits to flowers from insects which were more likely to effect pollination.

The primary purpose of most of the pollinator visits, judged from the insect's position in the flower, was to feed on nectar. In addition, some of the bumblebees were collecting pollen from Pedicularis although they visited the flowers in a typical nectar feeding position: 13 of the bumblebees collected had pollen loads with a high content

Table 8.2-4. Summary of the observed insect visitors considered most likely to have been pollinators of the flowers of Pedicularis at the McConnell River.[1]

PEDICULARIS	INSECT POLLINATORS	TOTAL NUMBER OF INDIVIDUALS COLLECTED
sudetica	Helophilus borealis Staeg. (1968)	32
	H. groenlandicus O. Fabricius (1968)	1
	Bombus polaris Curt. (1965, 1968)	48
	B. sylvicola Kirby (1968)	3
parviflora	Helophilus borealis (1967, 1968)	2
	Bombus polaris (1968)	1
	B. sylvicola (1965)	1
lapponica	Bombus polaris (1968)	1
	B. sylvicola (1968)	1
labradorica	none observed	
flammea	none observed	

1. Criteria for pollinator classification given in the text.

(ca. 75%) of pollen from Pedicularis. The positions and activities of individuals of Bombus spp. and Helophilus spp. in the flowers, as described earlier, could presumably facilitate movement of pollen from the anthers to the stigma of the same flower, among flowers of the same plant and among plants. The relatively precise stigma contact and application of pollen on the dorsal side of bumblebees (nototribic pollination) which was observed primarily in

Pedicularis sudetica is similar to that found and illustrated by Macior (1968b, 1970) for P. sudetica (in Colorado) and for other species of Pedicularis such as P. canadensis, P. crenulata, and P. parryi.

If nectar feeding was a major reason for bumblebee or syrphid visits at the McConnell River, the lack of observed visits to the nectarless flowers of Pedicularis flammea is not surprising. However, the absence of nectar does not necessarily preclude bumblebee pollination in species of Pedicularis. For example, Macior (1968a, 1969, 1970) showed that worker bumblebees transported pollen among stigmas in nectarless populations of three species of Pedicularis while collecting only pollen. These workers hung from the galea and either removed pollen directly with their legs or vibrated pollen from the anthers onto their bodies.

Nevertheless, few or no pollinator visits were observed in three of the nectar containing species (Pedicularis labradorica, P. lapponica and P. parviflora; Table 8.2-4, Table 4.2-1). The relative rarity of observed visits to these plants may be attributed to such factors as the following: (1) a low availability of pollinators during the flowering period (e.g. only the queens of Bombus polaris and the queens and workers of B. sylvicola were known to be present when Pedicularis lapponica was flowering, (2) the sharing of the pollinators with other species of Pedicularis or with species in other genera, (3) a preference of the

pollinators present for other species and (4) inadequate observations.

For example, one possibility is that a primary disadvantage of the flowering periods of Pedicularis labradorica and P. parviflora in 1968 was that they overlapped with flowering in P. sudetica. The only visits of either Helophilus borealis or Bombus polaris to plants of Pedicularis parviflora were observed on 16 and 17 August (Table 8.2-5). Prior to this, on nine occasions bumblebees (Bombus polaris) visiting plants of Pedicularis sudetica approached nearby inflorescences of P. parviflora, circled them once or more, and then continued their visits to Pedicularis sudetica. Clearly the bees were aware of the existence of Pedicularis parviflora; but they appeared to continue foraging on Pedicularis sudetica on the same foraging trip and presumably on subsequent trips.

The observations in Table 8.2-5 also suggest that Helophilus borealis and Bombus polaris tended to feed almost entirely on Pedicularis sudetica during the first half of August. Visits of both Helophilus borealis and Bombus polaris to species other than Pedicularis sudetica appeared to coincide with the decline in relative abundance of flowering plants of Pedicularis sudetica. The diversification of feeding by Bombus polaris beginning on 17 August may also have been a reflection of the increasing population size of this species (newly emerged males and queens were now present, see Table 8.2-1) and its subsequent effect on the availability

Table 8.2-5. Summary of observed visits to flowers of all plant species by individuals of Helophilus and Bombus at the McConnell River in 1968. Evidence of visits is from collected specimens except where noted.

INSECT	PLANT	DATE
DIPTERA: Syrphidae		
Helophilus borealis	Pedicularis sudetica Willd.	8, 9, 10, 12, 14, 17, 18, Aug.
	P. parviflora Sm.	16 Aug.
	Epilobium latifolium L.	18 Aug.
H. groenlandicus	Saxifraga hirculus L.	1 Aug.
	Pedicularis sudetica	9 Aug.
HYMENOPTERA: Apidae		
Bombus spp.[1]	Oxytropis bellii (Britt.) Palibine	15, 16 July
	Q. maydelliana Trautv.	19, 20 July
Bombus sylvicola	Pedicularis lapponica L.	21 July
	P. sudetica	26 July, 4, 18 Aug.
	Astragalus alpinus L.	27 July
	Silene acaulis L.	17 Aug.
	Vaccinium vitis-idaea L.	18 Aug.
Bombus polaris	Dryas integrifolia Vahl.	17 July, 1 Aug.
	Pedicularis lapponica	22 July
	P. sudetica	25 July, 3, 9, 12, 14, 16, 17, 18, 21 Aug.
	P. parviflora	17 Aug.
	Vaccinium vitis-idaea	17 Aug.
	Epilobium latifolium	18 Aug.
	Potentilla palustris (L.) Scop.	18, 21 Aug.

1. Observed only, uncertain of the species of Bombus.

of nectar and pollen. By this time, however, plants of Pedicularis labradorica had already completed flowering.

A factor which might have contributed to the apparent preference of Bombus polaris and Helophilus borealis for Pedicularis sudetica was its relatively long flowering period (see Figure 8.2-1). Long flowering periods may exceed the "delay period" between first flowering and the first pollinator visits (Manning 1956) and result in a stronger binding of the relationship between visitor and flower, and consequently, a greater constancy of visits to that species (Faegri and van der Pijl 1966). Manning (1956) has recorded a delay of 12 to 13 days from the start of flowering in Cynoglossum officinale to the first bumblebee visits.

Other factors influencing the plant-pollinator relationship may involve: (1) access to nectar and (2) quantity and quality of nectar (Pedersen 1953). Judged from the position of the bumblebees in the flowers of Pedicularis sudetica, tongue lengths in the various castes must have been sufficient to reach the nectar. Since flowers of Pedicularis sudetica had longer corolla tubes than the other species of Pedicularis at the McConnell River (Table 4.2-1), it seems doubtful that nectar feeding would be a problem in the other species, unless (1) P. sudetica had a sufficiently greater quantity of nectar in the tube to reduce the "reaching length" to less than that in the flowers of the other species, or (2) bees were

able to enter further into the corolla tube, or (3) both. There was also no evidence at the McConnell River that bumblebees were stealing nectar by puncturing the calyx and corolla to reach it (described in Pedicularis lapponica in Norway, Lagerberg et al. 1957). Apparently the "fit" of bumblebees and corolla tubes was adequate at the McConnell River. The relative abundance of flowers and nectar in the various species of Pedicularis was not investigated at the McConnell River.

The observations of bumblebee visits to Pedicularis sudetica and P. lapponica augment records of bumblebee visits to these species in other areas (e.g. Mathiesen 1921, Richards 1927, Shumarin 1966, Lagerberg et al. 1957). The observations from the McConnell River are apparently the first records of bumblebee visits to Pedicularis parviflora. I know of no reports of bumblebee visits to either P. labradorica or P. flammea, and no visits were observed at the McConnell River in 1968.

These observations from the McConnell River appear to be the first which suggest that a syrphid, such as Helophilus borealis, may be an important pollen vector in any population or species of Pedicularis. From field observation, it appears that Helophilus borealis might transport more pollen and be a more effective pollinator of Pedicularis sudetica than bumblebees because (1) the fly's position in the flowers generally caused a greater release of pollen onto itself than even the large queen bumblebees,

and (2) the fly did not seem to be able to clean the pollen accumulation from the part of its thorax which touched the stigma during visits.

It is not known whether the Helophilus - Pedicularis relationship is more widespread than the McConnell River area; these findings, however, cast doubt on the hypothesis that Pedicularis might be self-pollinated if Bombus is absent in an area (Aurivillius 1883). The distributions of both of the species of Helophilus found at the McConnell River extend from the Canadian Arctic southward into the United States and eastward to Greenland (Curran and Fluke 1926, Vockeroth, personal communication). Thus, contact between these syrphids and several species of Pedicularis is presumably possible in other locations.

Finally, it should be stressed that the pollination activities reported here were based on observations primarily from a single season and cannot safely be extrapolated to other years. The quantity of pollinators seen in 1968, in contrast to the few pollinators seen in previous years, gave a subjective impression that Bombus polaris and Helophilus borealis were either exceptionally numerous in 1968 or that they were feeding more extensively on species of Pedicularis than in previous years.

8.3 Seed production, pollination and probable breeding systems

One of the reasons for low seed production or no seed production in Pedicularis, excluding predated inflorescences and inflorescences in which flowers did not reach anthesis,

could be inadequate or inappropriate pollination. Examples of low seed output (e.g. one to five seeds per plant) in undamaged plants are given in Table 8.3-1. The numbers of plants with no seeds were given in Table 7.1-1. These data show that Pedicularis flammea had the lowest percentage of undamaged attempts with one to five seeds (and three attempts with no seeds) whereas Pedicularis lapponica had the highest percentage of undamaged attempts with one to five seeds (and 15 attempts with no seeds).

In Table 8.3-2, the species of Pedicularis are listed according to the percentages of bagged plants found with seeds. Again Pedicularis flammea and P. lapponica occupy the

Table 8.3-1. The number and percentage of undamaged reproductive attempts with one to five seeds per attempt at the McConnell River, 1965-1968.

PEDICULARIS	NUMBER OF SEEDS PER REPRODUCTIVE ATTEMPT					TOTAL NUMBER OF ATTEMPTS WITH 1-5 SEEDS	TOTAL NUMBER OF UNDAMAGED ATTEMPTS	%
	1	2	3	4	5			
flammea	0	1	0	0	0	1	38	3%
parviflora	2	1	0	1	0	4	80	5%
labradorica	1	2	1	1	2	7	75	9%
sudetica	1	4	1	0	2	8	49	16%
lapponica	11	5	8	6	3	33	98	34%

Table 8.3-2. Estimates of the possibilities (+) of self-fertilization and of outcrossing in Pedicularis at the McConnell River based on seed production in bagged plants and observations of flower visitors.

PEDICULARIS	PERCENTAGE OF BAGGED PLANTS WITH SEEDS	POSSIBILITY OF SELF-FERTILIZATION	PRESUMED POLLEN VECTORS	POSSIBILITY OF OUTCROSSING
flammea	100%	+	none observed	?
labradorica	42% - 97%	+	none observed	?
parviflora	40%	+	Helophilus borealis	
			Bombus polaris	
			B. sylvicola	+
sudetica	19%	+	Helophilus borealis	
			H. groenlandicus	+
			Bombus polaris	
			B. sylvicola	
lapponica	0%	?	Bombus polaris	
			B. sylvicola	+

two extreme positions: all bagged plants of the former produced seeds, presumably by self-pollination and self-fertilization; none of the bagged plants of the latter produced seeds, presumably due to the failure of self-pollination or self-fertilization. Furthermore, although two species of pollen vectors have been observed for P. lapponica at the McConnell River, only one individual of each bumblebee species has actually been seen visiting its flowers. Thus, visits and pollination by bumblebees may be irregular or uncommon at the McConnell River. The implication from the results in Tables 8.3-1 and 8.3-2, is that lack of pollination or fertilization could have contributed substantially to the low seed output in some plants of Pedicularis lapponica and to the low reproductive efficiency of the species (8%). This contrasts with the situation in P. flammea where few plants had few seeds and seed production occurred despite the absence of pollinators in bagged plants. Thus, there is no evidence to suggest that lack of pollination or fertilization affected seed production in P. flammea.

The remaining three species of Pedicularis appear in an intermediate position (cf. Tables 8.3-1 and 8.3-2). For example, Pedicularis sudetica, the species with the second lowest percentage of bagged plants with seeds (19%) had the second highest percentage (16%) of undamaged attempts with one to five seeds (Table 8.3-1) and the highest percentage of incomplete reproducers (Table 7.1-1), although some of the incomplete reproducers aborted when the inflorescences were immature (i.e. before anthesis). Four species of pollen vectors have been identified for P.

sudetica; unfortunately no data on seed output were obtained in 1968, the only year when numerous pollinators were seen visiting its flowers. These results and observations at the McConnell River (excluding the incomplete reproducers which aborted when still immature) suggest that ineffectiveness of pollination could have contributed to the low seed output in individual plants and to the low reproductive efficiency in this species (2%).

Although only about 40% of the bagged plants of Pedicularis parviflora produced seeds, only four undamaged plants had between one and five seeds and only one plant had no seeds. This species also had the highest reproductive efficiency (40%) at the McConnell River. Three probable pollen vectors were identified at the McConnell River; however, visits of pollinators in 1968 were not as commonly observed in P. parviflora as in P. sudetica. Nevertheless, there is little evidence to suggest that inadequate pollination made an important contribution to the species' 40% reproductive efficiency.

In Pedicularis labradorica, variable frequencies of bagged plants produced seeds and no pollinators were observed. Seven undamaged plants had between one and five seeds and nine plants had no seeds. Thus, inadequate or inappropriate pollination could have contributed to the low seed output in some plants of this species and to its 7% reproductive efficiency.

Table 8.3-2 also summarizes the evidence which

suggests that possibilities for self-pollination and self-fertilization (autogamy and geitonogamy) exist in four species and possibilities for cross-pollination and cross-fertilization (xenogamy) exist in three species of Pedicularis at the McConnell River. Although the activities of pollen vectors could also transport pollen within and among flowers of the same plant, and thereby facilitate autogamy and geitonogamy, they at least provide a means of transporting pollen among plants which, following fertilization, could give rise to an array of new genotypes.

On the basis of the observations of pollen vectors (Section 8.2), it appears that the outcrossing features of the flowers of Pedicularis parviflora, P. lapponica and P. sudetica (see Section 4.2) are currently functional, rather than vestigial (cf. Mosquin 1966), at the McConnell River. In fact, experiments are needed, judged from the bagged plants without seeds, to determine whether all plants of these species are self-compatible or whether some, or all, plants actually require cross-pollination for seed production. There was no evidence to indicate that the outcrossing features of Pedicularis labradorica were functional at the McConnell River; some plants of this species might also have been self-incompatible.

Based on the evidence available here and assuming that reproduction is mainly sexual in the populations of Pedicularis studied, the breeding systems of these species at the McConnell River could range from mainly or even

wholly inbreeding (autogamy, geitonogamy, i.e. P. flammea) to mainly or even wholly outbreeding (xenogamy, i.e. P. lapponica). Pedicularis sudetica and P. parviflora appear to be both outbreeding and inbreeding species at the McConnell River; Pedicularis labradorica appears to be an inbreeding species at the McConnell River during the current period. Hence, there seem to be striking differences among the five species of Pedicularis in their "seed-reproducing phenotype" as related to their pollination syndromes and probable breeding systems at the McConnell River. The species with the highest and lowest reproductive efficiencies were ones which appear to be both outbreeding and inbreeding; the reproductive efficiencies obviously depend on a complex of factors of which pollination is only one.

Despite the apparently extreme differences in breeding systems in Pedicularis lapponica and P. flammea, the coefficients of variation among plants for the number of ovules per ovary were very similar (13.8% and 14.4%, respectively; Table 5.2.5). This suggests that Pedicularis flammea has maintained considerable genetic variability among plants even though it seems to be predominantly inbreeding, or that there is a large amount of phenotypic plasticity, or both; recent evidence indicates that populations of predominantly self-fertilized plants may have high levels of genetic variability and hence considerable genetic flexibility (Allard 1965, Kannenberg and Allard 1967).

Conversely, strong selection pressure may have reduced the amount of variation between plants of P. lapponica. The highest coefficient of variation among plants for number of ovules was found in Pedicularis sudetica (21.3%). At least some of this variability, judged from the pollen vectors of Pedicularis sudetica observed at the McConnell River, can plausibly be attributed to genetic differences arising from outcrossing.

Chapter 9

SUMMARY

1. A comparative field study (1965-1968) was made of the relative success of seed production and of some of the conditions contributing to reproductive failures in five species of Pedicularis occurring in an arctic location (the mouth of the McConnell River, N.W.T., Canada, 60°50'N, 94°25'W). Additional studies were conducted on four of the species at a subarctic location (Churchill, Manitoba). Sampling was designed to obtain estimates of levels of variation due to various sources (e.g. years, sites, plants).

2. At the McConnell River, four species of Pedicularis reproduced only by seeds (P. flammea L., P. labradorica Wirsing, P. parviflora Sm. and P. sudetica Willd.); a single species reproduced by seeds and rhizomes (P. lapponica L.). Most plants of all five species of Pedicularis had root attachments to other species of plants, and they were, therefore, presumed to be hemi-parasitic.

3. Flowers of most species were similar in size. Four of the species possessed nectar, scent, and herkagamous flowers, characteristics generally associated with out-crossing in the genus (exception: P. flammea).

4. Observation of marked plants at the McConnell River indicated that all five species were perennial but they varied in the number and frequency of reproductive attempts. Two species (P. labradorica and P. parviflora) generally attempted reproduction only once.

5. The potential seed production per reproductive attempt, estimated from numbers of ovules and flowers, averaged from 100 seeds in Pedicularis lapponica (per node) to 1,500 seeds in P. sudetica (per plant). The mean number of flowers per plant (1967) varied from 7.1 (P. flammea) to 42.9 (P. sudetica); the mean number of ovules per ovary (1968) varied from 11.4 (P. parviflora) to 41.4 (P. flammea).

6. Conditions were favorable, or adequate, for seed production at the McConnell River in each year of this study, for all species, with the possible exception of two species in 1968. The analyses of seed output data revealed more variability in seed production among randomly selected sites within a year than among years. The average number of seeds per plant, per reproductive attempt, over a three to four year period, ranged from 8 (P. lapponica) to 164 (P. parviflora); estimated reproductive efficiencies ranged from 2% (P. sudetica) to 40% (P. parviflora). Limited evidence from Churchill suggested that seed production there averaged at least 50% to 300% higher per species than at the McConnell River. The field observations suggested that two categories of reproductive attempts (termed the

incomplete reproducers, and the damaged plants) contributed to variation in seed production among plants and among sites, as well as to a reduction in reproductive efficiency.

7. The frequency of incomplete reproducers (undamaged plants with no seeds) differed significantly between sites for Pedicularis lapponica (1966) and for P. sudetica (1966 and 1967) and the sites with the highest frequencies of incomplete reproducers had the lowest mean seed output per plant. The overall frequency of incomplete reproducers over three to four years varied from 1% in Pedicularis parviflora (the species with the highest reproductive efficiency) to 17% in P. sudetica (the species with the lowest reproductive efficiency).

8. Two types of damage to reproductive parts of plants, designated as seed predation and capsule predation, were found in Pedicularis at both the McConnell River and at Churchill. The overall frequencies of damaged reproductive attempts at the McConnell River (excluding the incomplete reproducers) ranged from 26% in Pedicularis lapponica to 61% in P. sudetica. Significant differences in the frequency of damaged attempts and the types of damage were detected between sites, between years, between locations and between some species. Reproductive failure (no seed output) occurred in 12% (P. parviflora) to 65% (P. lapponica) of the damaged plants. In some comparisons (within a site), damaged plants had significantly fewer seeds than undamaged plants

(P. labradorica, P. lapponica); in other comparisons no statistical differences were detected (all species); and, in other comparisons damaged plants had significantly more seeds than undamaged plants (P. parviflora).

9. Insect exclusion experiments, repeated over two and three years at the McConnell River, revealed no differences in the frequency of bagged and control plants with seeds in all years in Pedicularis flammea and in two out of three years in P. labradorica. In P. sudetica and P. parviflora, plus P. labradorica in 1967, a significantly higher proportion of control plants than bagged plants produced seeds. No bagged plants of P. lapponica contained seeds. From observations of flowers and flower visitors to Pedicularis in 1968 at the McConnell River, four species of insects were identified as probable pollen vectors.

10. From these results, it was suggested that the variable reproductive efficiencies among species of Pedicularis at the McConnell River were associated with differing degrees of seed and capsule predation and with the effectiveness of pollination. Both conditions imply that biotic factors can have important effects on the success of seed production in some arctic plants.

Appendix A

GENERAL TABLES

Table A2.3-1. The reproductive survey sites, McConnell River.

YEAR	SITE	SPECIES OF PEDICULARIS SAMPLED	DESCRIPTION OF SITE[1].
1965	A1	flammea, labradorica, sudetica, lapponica	ridge, slope and hummocky lowland (1 m)
	A2	flammea, lapponica, sudetica	hummocky lowland (0.6 m)
	A3	labradorica, lapponica, parviflora, sudetica	ridge, slope and hummocky lowland with a shallow pond[2]. (1.5 m)
	A4	labradorica	ridge (0.5 m)
	A5	parviflora	lowland with an intermittent stream and a perennial pond (0.5 m)
1966-1968	1	flammea, lapponica, sudetica	ridge, slope and hummocky lowland (1 m)
	2	flammea, labradorica, lapponica, sudetica	ridge, slope and hummocky lowland with an intermittent stream (1 m)
	3	flammea, labradorica, lapponica, sudetica	ridge, slope and hummocky lowland with a shallow perennial pond (1 m)
	4	labradorica, parviflora	ridge and perennial pond (1 m)
	5	flammea, labradorica, lapponica	ridge, slope and hummocky lowland (1 m)
	6	parviflora, sudetica	lowland with a perennial pond (0.5 m)
	7	parviflora, sudetica	lowland with a perennial stream (0.5 m)
	8	labradorica, lapponica	ridge (0.5 m)
	9	parviflora	lowland with marsh (0.5 m)
	10	parviflora	lowland with marsh (0.5 m)
	11	flammea	ridge and slope (0.5 m)

1. Maximum range of elevation within a site (to the nearest 0.5 m) is given in parentheses.
2. pond = surface area < 10,000 m^2 (Peterken 1967).

Table A2.3-2. Reproductive survey sites, Churchill, Manitoba.

SITE	SPECIES OF PEDICULARIS SAMPLED	DESCRIPTION OF SITE[1].
1, 2	flammea, labradorica, lapponica, sudetica	ridge, slope and lowland (1m); willow scrub on ridge and slope, sedge meadow on the lowland
3	labradorica	lichen-covered mounds each with a top surface area of 1-2 m^2, in open black spruce-larch forest (1.5 m)
4	flammea, lapponica, sudetica	low ridge, slope, and lowland with a perennial pond (1 m); ridge with scattered black spruce and lichens, sedge meadow on lowland
5	labradorica, lapponica	lichen-covered mounds in open black spruce forest (1 m)

1. Maximum range in elevation within a site (to the nearest 0.5 m) is given in parentheses.

Table A4.4-1. The patterns of flowering (F), vegetative rosette (V), and death (M) in marked plants of Pedicularis flammea at the McConnell River and at Churchill.

(1) McConnell River

	PATTERNS[1].									
SITE	FVF	FVV	FVM	FM-	VFV	VFM	VVF	VVV	VVM	TOTAL
1	0	5	0	1	3	1	1	5	4	20
2	1	3	0	1	5	1	0	6	3	20
3	1	3	2	0	1	0	3	6	4	20
5	0	3	1	0	1	2	4	5	4	20
11	1	4	2	1	5	0	2	3	0	18
TOTAL:	3	18	5	3	15	4	10	25	15	98

(2) Churchill

	PATTERNS[1].					
SITE	FF	FV	FM	VF	VV	TOTAL
1	1	7	0	6	5	19
2	1	5	5	2	4	17
4	0	11	2	3	2	18
TOTAL:	2	23	7	11	11	54

1. Patterns are given in sequence by years (1966-1967-1968 at the McConnell River, 1966-1967 at Churchill).

Table A4.4-2. The patterns of flowering (F), vegetative rosette (V), and death (M) in marked plants of Pedicularis sudetica at the McConnell River and at Churchill.

(1) McConnell River

SITE	PATTERNS[1]. FFF	FFV	FFM	FVF	FVV	FVM	FM-	VFF	VFV	VVF	VVV	TOTAL
1	4	4	0	1	1	0	0	1	3	3	2	19
2	6	2	0	4	2	0	0	4	0	0	2	20
3	3	1	0	1	3	0	0	3	4	2	3	20
6	11	2	0	2	1	2	0	0	0	1	1	20
7	7	1	1	10	1	0	0	0	0	0	0	20
TOTAL:	31	10	1	18	8	2	0	8	7	6	8	99

(2) Churchill

SITE	PATTERNS[1]. FF	FV	FM	VF	VV	VM	TOTAL
1	2	3	2	1	1	0	9
2	1	2	2	6	11	1	23
4	2	10	8	1	2	1	24
TOTAL:	5	15	12	8	14	2	56

1. Patterns are given in sequence by years (1966-1967-1968 at the McConnell River, 1966-1967 at Churchill).

Table A4.4-3. The patterns of flowering (F), vegetative rosette (V), and death (M) at marked nodes of rhizomes of Pedicularis lapponica at the McConnell River and at Churchill.

(1) McConnell River

	PATTERNS[1].											
SITE	FUn-[2].	FFF	FFV	FFUn	FFM	FVF	FVV	FVM	FM-	VFV	VVV	FVUn	TOTAL
1	1	1	0	0	0	1	10	2	2	0	0	3	20
2	1	0	0	0	0	4	5	3	5	0	0	2	20
3	0	1	3	1	2	0	3	1	3	0	1	5	20
5	1	0	1	0	0	3	8	2	1	1	1	2	20
8	0	2	1	0	1	0	4	3	4	0	0	5	20
TOTAL:	3	4	5	1	3	8	30	11	15	1	2	17	100

(2) Churchill

	PATTERNS[1].								
SITE	FF	FV	FM	FUn	VF	VV	VM	VUn	TOTAL
1	1	3	1	0	4	7	1	8	25
2	2	3	2	0	0	9	8	1	25
4	1	3	4	2	0	5	2	8	25
5	0	3	2	0	0	9	7	4	25
TOTAL:	4	12	9	2	4	30	18	21	100

1. Patterns are given in sequence by years (1966-1967-1968 at the McConnell River, 1966-1967 at Churchill).
2. Un = uncertain of identity of plant. "Un" classes were excluded from the summary of data in Table 4.4-5.

Table A5.1-1. Estimates of skewness on transformed data of the number of flowers per plant for three species of Pedicularis.

PEDICULARIS	ESTIMATES OF SKEWNESS[1].	
	LOG_{10} TRANSFORMATION	SQUARE ROOT TRANSFORMATION
flammea	- 0.34 ns	0.21 ns
labradorica	- 0.69 ***	0.28 ns
parviflora	- 0.79 ***	- 0.03 ns

1. The reference for calculation is given in Table 2.4-1.

Table A5.2-1. The number of ovules per ovary in Pedicularis parviflora, P. lapponica, and P. labradorica at the McConnell River (1968).

PEDICULARIS PARVIFLORA						PEDICULARIS LAPPONICA						PEDICULARIS LABRADORICA					
DATA					MEAN	DATA					MEAN	DATA					MEAN
9	10	10	10	7	9.2	12	10	10	9	8	9.8	17	18	13	14	13	15.0
12	7	10	8	9	9.2	11	14	8	9	10	10.4	13	16	18	19	14	16.0
9	8	12	10	9	9.6	12	13	13	7	9	10.8	16	17	17	17	17	16.8
9	11	11	10	9	10.0	12	13	11	11	9	11.2	16	16	17	17	18	16.8
12	11	11	8	10	10.4	12	9	11	13	12	11.4	16	16	16	18	18	16.8
10	10	12	11	9	10.4	12	13	11	11	11	11.6	19	16	15	19	18	17.4
12	12	9	9	11	10.6	12	12	12	12	12	12.0	21	17	15	18	19	17.8
10	12	10	12	9	10.6	12	13	12	12	12	12.4	20	20	16	17	18	18.2
10	12	12	10	11	11.0	14	13	12	12	11	12.4	17	19	19	19	18	18.4
4	12	11	17	12	11.2	15	15	14	12	7	12.6	20	19	18	17	19	18.6
10	10	12	11	13	11.2	11	13	13	14	14	13.0	18	17	20	19	20	18.8
9	10	13	13	11	11.2	13	13	14	14	14	13.6	19	20	21	15	21	19.2
13	12	11	10	11	11.4	14	15	14	14	13	14.0	21	18	20	18	20	19.4
10	11	11	13	13	11.6	16	14	13	15	13	14.2	19	19	20	20	19	19.4
11	12	14	15	11	12.6	14	13	15	16	14	14.4	19	20	23	19	18	19.8
12	12	15	10	14	12.6	14	16	17	15	12	14.8	20	19	20	18	22	19.8
12	13	12	13	14	12.8	15	13	16	15	16	15.0	21	20	22	20	20	20.6
16	12	15	12	12	13.4	15	15	15	16	18	15.8	21	21	23	19	19	20.6
12	14	12	14	16	13.6	19	15	16	16	13	15.8	22	19	25	20	18	20.8
14	18	12	16	17	15.4	17	15	15	17	17	16.2	21	21	19	24	22	21.4

Table A5.2-2. The number of ovules per ovary in Pedicularis sudetica and P. flammea at the McConnell River (1968).

PEDICULARIS SUDETICA DATA					MEAN	PEDICULARIS FLAMMEA DATA					MEAN
14	15	13	13	12	13.4	28	24	26	30	30	27.6
22	28	28	27	30	27.0	36	33	32	38	34	34.6
26	34	26	28	26	28.0	25	36	36	36	40	34.6
32	31	26	30	32	30.2	36	38	32	37	34	35.4
32	30	28	34	31	31.0	38	28	38	38	38	35.6
35	32	30	32	30	31.8	30	36	36	36	42	36.0
32	34	30	30	33	31.8	36	38	36	38	36	36.8
30	36	34	30	34	32.8	38	40	40	34	40	38.4
34	32	32	30	36	32.8	43	36	44	38	40	40.2
32	34	32	34	32	32.8	42	38	40	42	40	40.4
34	30	36	36	32	33.6	45	44	46	40	40	43.0
38	36	36	34	38	36.4	44	50	36	44	42	43.2
38	36	40	42	40	39.2	42	45	45	42	48	44.4
41	42	38	39	42	40.4	48	38	50	46	42	44.8
38	38	42	42	44	40.8	42	46	44	48	44	44.8
38	42	42	42	44	41.6	44	44	46	50	46	46.0
44	44	42	40	44	42.8	58	48	40	48	42	47.2
44	46	42	42	42	43.2	44	48	50	50	50	48.4
47	42	46	40	45	44.0	46	50	52	52	52	50.4
50	38	44	40	50	44.4	48	50	50	50	54	50.4

Table A6.1-1. The number of seeds (per plant) per reproductive attempt in Pedicularis flammea.[1]

YEAR/ LOCATION[2]	SITE	SAMPLE SIZE	SEEDS PER PLANT	MEAN	MEDIAN
1965/ Mc	A1	10	0 0 0 0 1 6 31 35 67 97	23.7	3.5
	A2	10	0 26 30 36 49 54 86 107 162 319	86.9	51.5
1966/ Mc	1	6	24 26 52 101 202 220	104.2	76.5
	2	5	0 2 90 92 159	68.6	90.0
	3	7	0 0 0 4 7 13 84	15.4	4.0
	5	3	2 7 94	34.3	7.0
	11	9	0 0 0 1 1 3 3 9 43	6.7	1.0
1967/ Mc	1	4	0 189 198 206	148.2	193.5
	2	6	0 2 32 37 78 98	41.2	34.5
	3	1	14	-	-
	5	3	31 49 61	47.0	49.0
	11	5	38 84 84 90 161	91.4	84.0
1968/ Mc	1	1	405	-	-
	2	1	204	-	-
	3	2	95 110	102.5	102.5
	5	2	0 81	40.5	40.5
	11	2	0 45	22.5	22.5
1966/ Ch	1	9	79 83 124 130 134 144 232 323 447	188.4	143.0
	2	12	0 0 5 6 8 13 19 23 103 139 203 389	75.7	16.0
	4	17	0 0 0 1 2 4 4 5 6 19 19 29 33 35 42 48 109	20.9	6.0

1. Underlining indicates damaged plants.
2. Mc = McConnell River, Ch = Churchill.

Table A6.1-2. The number of seeds (per plant) per reproductive attempt in Pedicularis labradorica.[1]

YEAR/ LOCATION[2]	SITE	SAMPLE SIZE	SEEDS PER PLANT	MEAN	MEDIAN
1965/ Mc	A1	10	0 0 13 33 49 54 80 116 259 532	113.6	51.5
	A3	10	6 12 14 25 33 46 54 77 104 110	48.1	39.5
	A4	7	0 0 22 32 50 53 83	34.3	32.0
1966/ Mc	2	17	0 3 6 8 15 32 33 36 39 43 57 60 65 68 70 87 92	42.0	39.0
	3	9	0 0 0 5 9 16 28 72 115	27.2	9.0
	4	17	0 2 3 5 6 8 10 16 17 20 22 24 30 48 53 54 105	24.9	17.0
	5	11	0 0 0 1 6 10 33 33 44 54 367	49.8	10.0
	8	20	0 8 9 19 21 38 40 69 71 73 77 90 92 101 115 119 126 131 133 136	73.3	75.0
1967/ Mc	3	10	4 5 11 14 27 43 46 54 96 141	44.1	35.0
	4	4	1 2 15 24	10.5	8.5
	5	7	0 0 3 7 12 33 35	12.9	7.0
	8	3	0 14 31	15.0	14.0
1966/ Ch	1	16	0 1 7 10 12 20 38 42 43 46 65 66 70 85 90 192	49.2	42.5
	2	13	0 3 7 8 11 12 23 29 32 48 102 165 318	58.3	23.0
	3	25	21 26 32 35 41 42 49 51 70 77 81 116 119 131 133 137 139 140 211 298 317 346 457 534 672	171.0	119.0
	5	20	0 0 0 0 4 9 11 17 25 28 30 30 38 50 73 81 86 123 200 264	53.4	29.0

1. Underlining indicates damaged plants.
2. Mc = McConnell River, Ch = Churchill.

Table A6.1-3. The number of seeds (per node of rhizome) per reproductive attempt in Pedicularis lapponica.[1].

YEAR/ LOCATION[2].	SITE	SAMPLE SIZE	SEEDS PER NODE	MEAN	MEDIAN
1965/ Mc	A1	10	0 2 5 7 8 9 12 16 18 19	9.6	8.5
	A2	10	0 1 1 3 9 14 16 21 24 26	11.5	11.5
	A3	10	0 0 0 0 0 1 2 12 28 32	7.5	0.5
1966/ Mc	1	20	0 1 2 5 7 7 7 8 9 9 10 13 15 16 19 21 29 38 39	13.2	9.0
	2	20	0 0 0 1 1 2 2 3 3 3 5 8 8 12 13 15 18 20 23 26	8.1	4.0
	3	19	0 0 0 0 0 0 0 0 0 0 1 2 2 3 4 4 4 5 11	1.9	0.0
	5	18	0 0 0 0 0 0 0 0 0 3 4 6 8 10 10 10 15 24	5.0	1.5
	8	20	0 0 1 3 4 4 6 7 8 8 9 10 11 11 13 18 20 20 22 36	10.5	8.5
1967/ Mc	3	7	0 0 1 1 3 4 6	2.1	1.0
	5	2	0 3	1.5	1.5
	8	4	1 1 7 27	9.0	4.0
1968/ Mc	1	3	0 8 18	8.7	8.0
	2	4	0 13 16 56	21.2	14.5
1966/ Ch	1	5	0 11 15 39 43	21.6	15.0
	2	7	0 0 0 30 38 39 41	21.1	30.0
	4	9	0 0 0 0 5 8 9 16 29	7.4	5.0
	5	5	0 2 5 11 14	6.4	5.0

1. Underlining indicates damaged plants.
2. Mc = McConnell River, Ch = Churchill.

Table A6.1-4. The number of seeds (per plant) per reproductive attempt in Pedicularis parviflora at the McConnell River.[1]

YEAR	SITE	SAMPLE SIZE	SEEDS PER PLANT[2].	MEAN	MEDIAN
1965	A3	10	4 18 54 58 67 78 105 187 466 882	191.9	72.5
	A5	19	1 6 22 25 35 35 37 41 108 117 176 227 236 241 287 300 320 449 557	169.5	117.0
	4	20	9 24 44 53 63 64 69 81 101 149 188 206 268 295 356 360 368 400 423 580	205.0	168.5
	6	20	0 0 0 0 0 11 11 16 27 54 58 59 63 86 89 91 131 195 266 355	75.6	56.0
	7	20	2 9 10 10 17 18 25 39 42 51 55 55 58 61 69 72 126 152 223 596	84.5	53.0
	9	20	0 32 57 70 81 100 130 135 143 147 166 180 220 224 375 461 496 718 1,002 1,132	293.6	156.5
	10	20	0 0 13 13 54 74 77 84 89 98 103 117 131 140 167 193 231 260 718 884	172.3	100.5
1967	7	5	1 15 30 40 127	42.6	30.0
	9	3	23 30 608	220.3	30.0
	10	2	37 76	56.5	56.5

1. Underlining indicates damaged plants.

Table A6.1-5. The number of seeds (per plant) per reproductive attempt in Pedicularis sudetica.[1]

YEAR/ LOCATION[2]	SITE	SAMPLE SIZE	SEEDS PER PLANT	MEAN	MEDIAN
1965/ Mc	A1	10	0 0 2 3 14 14 18 28 55 71	20.5	14.0
	A2	8	0 0 0 0 9 11 13 54	10.9	4.5
	A3	10	4 11 16 80 86 103 133 168 188 366	115.5	94.5
1966/ Mc	1	11	0 2 3 5 5 15 16 18 21 36 50	15.5	15.0
	2	14	0 0 0 0 14 22 36 76 80 95 110 110 113 201	61.2	99.3
	3	8	0 0 0 0 0 0 0 9	1.1	0.0
	6	18	0 0 0 0 0 0 0 0 0 0 0 0 1 1 4 6 9 21	2.3	0.0
	7	20	0 0 2 2 3 4 7 7 8 10 12 22 42 50 51 57 62 64 73 126	30.1	11.0
1967/ Mc	1	11	0 2 2 5 6 6 8 9 12 18 50	10.7	6.0
	2	12	0 8 14 15 18 32 39 43 76 83 89 121	44.8	35.5
	3	11	0 0 0 0 0 0 0 0 5 16 32	4.8	0.0
	6	10	1 3 12 26 27 28 42 54 59 64	31.6	27.5
	7	9	1 0 7 14 23 37 85 92 95	39.3	23.0
1966/ Ch	1	6	0 27 44 83 105 215	79.0	63.5

1. Underlining indicates damaged plants.
2. Mc = McConnell River, Ch = Churchill.

Table A6.1-6. Tests of homogeneity of variances among sites sampled in several years applied to data on seed output using a count scale, a logarithmic scale and a square root scale.[1].

PEDICULARIS		ADJUSTED CHI SQUARE[2].		
	df	COUNTS	$\sqrt{Y + 0.5}$	LOG_{10} Y + 1
flammea	7	30.31 **	8.99 ns	10.11 ns
labradorica	9	92.29 **	24.90 **	13.30 ns
lapponica	7	32.73 **	12.06 ns	6.19 ns
parviflora	6	34.72 **	7.87 ns	10.09 ns
sudetica	12	174.04 **	57.41 **	15.25 ns

1. The data were coded as $\log_{10} Y + 1$, or $\sqrt{Y + 0.5}$, since it included zeros (Sokal and Rohlf 1969).
2. Bartlett's test of homogeneity of variance.

Table A7.21-1. The frequency of damaged (D) undamaged (UD) reproductive attempts in marked plants of Pedicularis in each site.

		PEDICULARIS															
LOCATION	YEAR	FLAMMEA			LABRADORICA			LAPPONICA			PARVIFLORA			SUDETICA			
		SITE	D	UD	SITE	D	UD	SITE	D	UD	SITE	D	UD	SITE	D	UD	
McConnell	1965	A1	10	0	A1	0	8	A1	1	8	A3	2	8	A1	6	2	
		A2	3	7	A2	3	7	A2	1	9	A5	6	13	A2	3	3	
					A3	1	4	A3	5	3				A3	9	1	
	1966	1	2	4	2	8	9	1	4	15	4	9	11	1	7	4	
		2	2	2	3	6	2	2	3	15	6	8	12	2	9	4	
		3	6	1	4	5	12	3	6	8	7	9	11	3	2	0	
		5	3	0	5	7	3	5	8	9	9	9	11	6	13	0	
		11	8	1	8	10	10	8	3	17	10	12	8	7	19	1	
	1967	1	0	3	3	0	10	1	0	1	7	3	2	1	0	10	
		2	0	5	4	1	3	3	1	5	9	0	3	2	3	8	
		3	0	1	5	0	5	5	2	0	10	0	2	3	2	2	
		5	0	3	8	0	2	8	0	4				6	0	10	
		11	0	5										7	4	4	
Churchill	1966	1	0	9	1	5	11	1	0	5	--	--	--	1	0	5	
		2	6	5	2	4	9	2	3	4				2	4	1	
		4	11	6	3	3	22	4	5	9				4	19	1	
					5	4	16	5	1	4							
	1967	1	4	3	1	1	1	1	0	5	--	--	--	1	1	1	
		2	1	2	2	2	0	2	0	2				2	6	0	
		4	2	1	3	1	2	4	1	0				4	0	2	
					5	0	1										

Table A7.21-2. The frequency of seed (Se) and capsule (Cap) predation in marked plants of Pedicularis in each site.

		PEDICULARIS														
LOCATION	YEAR	FLAMMEA			LABRADORICA			LAPPONICA			PARVIFLORA			SUDETICA		
		SITE	Se	Cap	SITE	Se	Cap	SITE	Se	Cap	SITE	Se	Cap	SITE	Se	Cap
McConnell	1965	A1	2	8	A1	0	0	A1	1	0	A3	2	0	A1	4	2
		A2	0	3	A2	0	3	A2	0	1	A5	6	0	A2	2	1
					A3	2	0	A3	2	3				A3	9	0
	1966	1	2	0	2	6	2	1	4	0	4	9	0	1	7	0
		2	2	0	3	4	2	2	2	1	6	4	4	2	7	2
		3	5	1	4	2	3	3	1	5	7	7	2	3	1	1
		5	3	0	5	4	3	5	0	8	9	9	0	6	9	4
		11	1	7	8	9	1	8	1	2	10	12	0	7	16	3
	1967	no damage			3	0	0	1	0	0	7	3	0	1	0	0
					4	1	0	3	0	1	9	0	0	2	3	0
					5	0	0	5	0	2	10	0	0	3	2	0
					8	0	0	8	0	0				6	0	0
														7	4	0
Churchill	1966	1	0	0	1	1	4	1	1	0	--	--	--	1	0	0
		2	2	4	2	2	2	2	0	3				2	0	4
		4	6	5	3	3	0	4	0	4				4	0	19
					5	0	4	5	0	0						
	1967	1	1	3	1	0	1	1	0	0	--	--	--	1	1	0
		2	1	0	2	0	2	2	0	0				2	0	6
		4	0	2	3	1	0	4	0	1				4	0	0
					5	0	0	5	0	0						

Table A8.1-1. The number of bagged plants and control plants of Pedicularis with seed(s) at the McConnell River.

		BAGGED PLANTS		CONTROL PLANTS	
PEDICULARIS	YEAR	SAMPLE SIZE	WITH SEEDS	SAMPLE SIZE	WITH SEEDS
flammea	1967	34	34	19	17
	1968	12	12	19	19
labradorica[1]	1966	30	29	50	50
	1967	26	11	24	21
	1968	5	4	19	19
lapponica	1966	48	0	50	46
	1967	35	0	14	13
	1968	9	0	20	18
parviflora	1966	9	3	50	50
	1967	28	10	10	10
	1968	10	6	19	19
sudetica	1966	43	9	50	45
	1967	29	2	53	43
	1968	14	2	18	18

1. Results differ between years. See text.

Table A8.1-2. The number of seeds per capsule in bagged and control plants of Pedicularis flammea at the McConnell River in 1968.

BAGGED PLANTS (12)			CONTROL PLANTS (19)		
NUMBER OF CAPSULES	NUMBER OF SEEDS PER CAPSULE		NUMBER OF CAPSULES	NUMBER OF SEEDS PER CAPSULE	
	RANGE	MEAN		RANGE	MEAN
2	15 - 17	16.0	5	0 - 16	3.2
5	13 - 19	16.4	5	0 - 19	7.2
6	5 - 21	17.2	5	0 - 19	11.0
4	13 - 21	17.5	10	0 - 33	13.5
4	7 - 23	17.5	11	12 - 17	13.7
4	16 - 20	18.0	5	0 - 31	15.0
8	10 - 25	20.9	12	9 - 21	15.1
5	16 - 27	21.2	11	2 - 25	15.6
7	18 - 25	22.6	9	5 - 24	16.7
8	15 - 29	25.0	6	9 - 27	16.7
13	4 - 39	25.6	5	8 - 23	17.0
9	20 - 32	27.2	9	12 - 27	19.4
			7	11 - 25	19.6
			5	18 - 25	20.6
75	4 - 39	20.4	12	7 - 35	21.9
			5	8 - 29	22.6
			6	0 - 36	25.5
			16	0 - 38	25.8
			2	30 - 33	31.5
			146	0 - 38	17.5

Table A8.1-3. Tests of homogeneity of variance (Bartlett's test) in the number of seeds per capsule among control plants of Pedicularis flammea at the McConnell River (1968).

TYPE OF DATA	df	CHI SQUARE
Original counts	18	47.30 **
Transformed counts		
Square root Y + 0.5	18	66.68 **
Log_{10} Y + 1	18	111.54 **

Table A8.1-4. The number of seeds per capsule in 20 control plants of Pedicularis lapponica at the McConnell River in 1968.

NUMBER OF CAPSULES	NUMBER OF SEEDS PER CAPSULE	
	RANGE	MEAN
5	0	0.0
5	0	0.0
8	1 - 3	2.0
7	0 - 5	2.3
5	0 - 5	3.0
4	1 - 4	3.2
8	0 - 6	3.5
2	3 - 4	3.5
8	2 - 6	3.9
4	2 - 6	4.0
3	3 - 5	4.0
2	3 - 5	4.0
10	2 - 6	4.1
4	2 - 7	4.5
5	4 - 6	4.8
3	4 - 6	5.0
5	3 - 8	5.4
2	5 - 6	5.5
12	4 - 7	6.2
8	4 - 8	7.0
110	0 - 8	3.9

Table A8.1-5. The number of seeds per capsule in bagged and control plants of Pedicularis labradorica at the McConnell River in 1968.

BAGGED PLANTS			CONTROL PLANTS		
NUMBER OF CAPSULES	NUMBER OF SEEDS PER CAPSULE		NUMBER OF CAPSULES	NUMBER OF SEEDS PER CAPSULE	
	RANGE	MEAN		RANGE	MEAN
10	0	0.0	9	2 - 10	4.9
8	0 - 3	1.0	2	0 - 10	5.0
10	0 - 16	5.6	37	2 - 9	5.4
8	7 - 18	12.9	13	3 - 11	6.8
11	7 - 18	13.3	13	2 - 10	7.3
			29	4 - 11	7.7
			36	1 - 14	8.5
47	0 - 18	6.6	8	7 - 11	9.0
			7	4 - 11	9.0
			92	2 - 16	9.1
			12	4 - 12	9.1
			15	4 - 14	9.3
			7	7 - 11	9.3
			5	7 - 12	9.4
			26	5 - 13	9.9
			14	7 - 14	10.4
			65	3 - 13	10.6
			11	8 - 14	11.4
			25	6 - 18	12.8
			426	0 - 18	8.6

Appendix B

FIELD AREAS

1. The McConnell River

The mouth of the McConnell River (60°50'N, 94°25'W) is located on a low and poorly drained coastal plain on the west side of Hudson Bay near Eskimo Point, Northwest Territories, Canada. The study area includes the south branch of the river, the adjacent flood plain, and the river delta (Figure B-1).

The Hudson Bay region was beneath the central zone of the Laurentide ice sheet during the last glaciation (Wisconsin) and was downwarped during ice occupation. It was inundated by salt water during the recession of the ice (about 7-8,000 years ago, Craig 1969) and subsequently has been, and still is, rebounding (Lee 1959, 1968, Barnett 1966, Craig 1969, Andrews 1969). Thus, the study area at the McConnell River became a terrestrial environment within the last few thousand years, following recession of the Tyrell Sea, and the elevation of the area above sea level is still changing.

Glaciation and marine submergence had considerable effect on landforms and surficial deposits at the mouth of the McConnell River (Lee 1959). Uplands are represented by a few beach ridges and eskers. The bedrock, primarily of

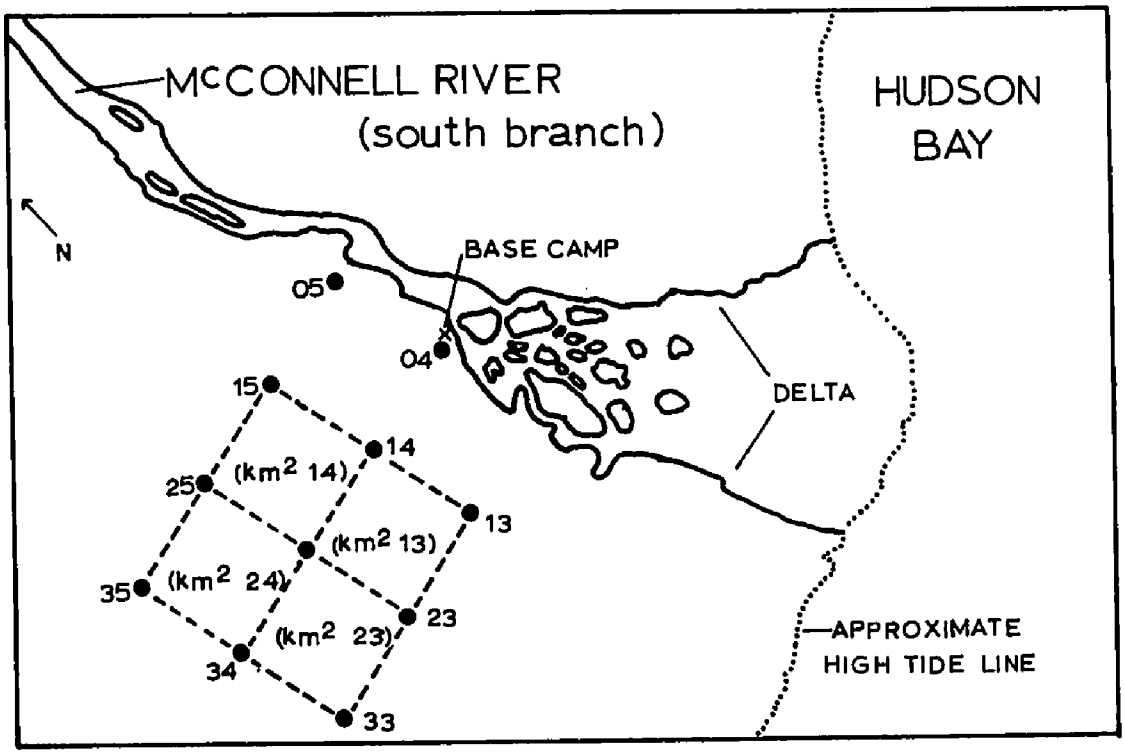

Figure B-1. Location of the McConnell River study area and the permanent grid used for sampling. Numbered poles (●) are 1 km apart.

Precambrian age (Lord 1953), is overlain by glacial till, marine deposits (silts, clays) and river deposits (sands, silts). The till has been reworked by marine action and subsequent deposits have been reworked by the river and by frost action.

The soils within the study area are predominantly Gleysols and Regosols (Day 1964 and personal communication). At the McConnell River, the Gleysols occur in poorly drained sites and possess a grayish mineral layer which is usually overlain by an organic layer of virtually undecomposed plant materials (similar to "tundra soils" of Tedrow 1968). The Regosols occur in imperfectly to well drained sites but lack any significant horizon development. They consist of a mineral layer which is frequently overlain by a partially decomposed organic layer. Organic soils (bog soils, Tedrow 1968) occur in a few sites within the study area.

Perennially frozen ground (permafrost) is continuous at the McConnell River (Brown 1960) and contributes to the wetness of the soils by impeding drainage and by thawing. The depth of the seasonal thaw (the active layer) varies depending on soil characteristics, moisture conditions and the amount and nature of the vegetative cover. In early August 1968, the depth of the active layer ranged from about 15 cm in peaty organic soils to greater than 80 cm on gravel ridges.

Climatic summaries for the nearest coastal meterological stations to the north (Chesterfield) and south (Churchill

Airport) of the McConnell River are given in Table B-1. Conditions at the McConnell River are expected to be somewhere between the two. In general, mean daily temperatures above freezing occur from June through September, and July and August are free of days with measurable snowfall. Low summer temperatures along the shores of Hudson Bay are attributed to the cooling influence of Hudson Bay, which may be congested with ice as late as mid-July (Thompson 1968).

Selected characteristics of the environment within the McConnell River study area, taken from base camp records, are shown in Table B-2. The percent snow cover is based on the proportion of steps in snow along a 4 km transect (04-14-15-05-04 of the permanent grid, Figure B-1). Air temperatures (1.5 m above the ground surface) and ground surface temperatures were recorded using unshielded maximum and minimum thermometers in 1965 and 1966 and a recording thermograph with unshielded probes (Dickson Minicorder) in 1967 and 1968. The thermometers and probes were positioned above (air) and at ground level within dwarf shrub vegetation (Betula glandulosa Michx. and Vaccinium uliginosum L.) at the edge of the ridge occupied by the base camp. These readings give one approximation of the local thermal conditions. The air temperatures given here in Table B-2 are not directly comparable with those in Table B-1 since the former were recorded from exposed instruments and the latter were recorded within a standard thermometer screen.

Table B-1. Climatic summaries from the nearest coastal meteorological stations north (Chesterfield = 1) and south (Churchill Airport = 2) of the McConnell River, N.W.T. (1931 - 1960).[1].

	STATION	JAN.	FEB.	MAR.	APR.	MAY	JUNE	JULY	AUG.	SEPT.	OCT.	NOV.	DEC.	YEAR
Temp. (C)														
Mean daily maximum	(1)	-28.0	-28.5	-21.3	-11.9	-2.7	5.6	13.1	12.0	5.1	-3.0	-13.8	-22.3	- 7.9
	(2)	-23.7	-22.2	-20.3	- 6.3	1.0	10.1	17.1	15.7	8.6	1.7	- 8.1	-17.8	- 3.3
Mean daily minimum	(1)	-35.2	-35.4	-29.4	-21.1	-9.4	-0.4	4.5	5.0	0.4	-8.6	-21.4	-30.3	-15.1
	(2)	-31.3	-30.6	-24.4	-15.2	5.7	1.5	6.9	7.6	2.8	-3.8	-15.3	-26.0	-11.1
Mean daily	(1)	-31.6	-32.0	-25.4	-16.4	-6.1	2.6	8.8	8.5	2.8	-5.7	-17.6	-26.3	-11.5
	(2)	-27.5	-26.4	-19.8	-10.7	-2.3	5.8	12.0	11.6	5.7	-1.1	-11.7	-21.9	- 7.2
Mean snowfall (mm)	(1)	84	86	114	165	104	23	0	T	36	203	203	163	1,181
	(2)	127	140	165	251	165	18	T	0	36	246	381	226	1,755
Number days with snowfall	(1)	6	5	7	7	6	1	0	0	2	8	9	8	59
	(2)	9	9	10	11	10	1	0	0	2	11	17	13	93

1. Thompson 1962, 1968; Meteorological Branch 1965a, 1965b, 1965c; Key: Temp. = temperature, T = trace (snowfall).

Table B-2. Environmental data from the McConnell River.

CHARACTERISTIC[1].	YEAR							
	1965		1966		1967		1968	
Snow cover 50%	1 June		30 May		31 May		8 June	
0%	9 and 14 June		10 June		3 June		14 June	
First flow in river	3 June		30 May		1 June		2 June	
Approximate temperatures (C)	Air	Ground	Air	Ground	Air	Ground	Air	Ground
June 7 - 30								
Mean maximum	6.6	11.1	17.7	-	12.3	21.4	11.8	20.4
Mean minimum	1.3	-2.5	0.5	-	1.5	0.7	2.3	1.0
July 1 - 31								
Mean maximum	14.9	18.0	18.8	-	18.9	31.3	20.3	28.1
Mean minimum	6.6	2.8	5.3	-	7.2	7.4	7.6	4.9
August 1 - 12								
Mean maximum	14.2	16.9	18.5	-	21.3	33.6	17.3	23.2
Mean minimum	7.2	1.4	6.2	-	8.3	8.6	5.5	3.2

1. See text for description of methods.

The following points can be noted from Table B-2. The land surface within the study area became free of snow in early June, shortly after water began flowing in the McConnell River. Comparisons of the maximum air temperatures between pairs of years when measurements were recorded by the same technique, suggest that 1966 was warmer than 1965, especially in June, and that 1967 and 1968 were very similar in June and July but early August was cooler in 1968 than in 1967.

The vegetation within the McConnell River study area is continuous except for small areas on the ridges and more extensive areas in the river delta and in seasonal streams and ponds. The predominant vegetation in the upland and well drained areas consists of dwarf shrubs (<50 cm high); the predominant vegetation in the lowlands and poorly drained areas consists of sedges and grasses.

2. Churchill, Manitoba

A secondary field study area was located near Churchill, Manitoba, on the Hudson Bay Lowlands about 250 km south of the McConnell River. The vegetation in this area is transitional between forest and tundra. Selected climatic data from Churchill were given in Table B-1. Comparable data are not available for the mouth of the McConnell River; it is presumed that Churchill has, in general, a slightly milder climate than the McConnell River. More detailed descriptions of the climate, vegetation, topography and

geology of this area are available in the literature (Williams 1948, Cheney and Beckel 1955, Ritchie 1956, 1957, Beckel 1967 and others). Observations and seed collections were made in an area bounded on the west by the Churchill River and extending 8 km east of Fort Churchill, along a roadway approximately parallel to the Hudson Bay coast.

Appendix C

SEXUAL REPRODUCTION IN THE GENUS PEDICULARIS

The limited direct and indirect evidence available for the genus Pedicularis suggests that reproduction by seed is probably, or basically, sexual. Observations of the penetration of the embryo sac by the pollen tube in Pedicularis sylvatica and P. palustris have been summarized by Sprague (1960). According to Jørgensen, Sørensen, and Westergaard (1958), when lacking more complete evidence (e.g. embryological studies and castration experiments), the probability of agamospermy may be inferred to be high in plants which normally set seed but have either (1) highly defective pollen, or (2) an odd multiple of the basic chromosome number (or are aneuploid). Hence, Jørgensen et al. (1958) classified all species of Pedicularis in Greenland, including Pedicularis flammea, P. lapponica and P. labradorica, as sexual since the plants of the various species set seed, did not have highly defective pollen, and were diploid.

On the basis of observed seed production, preliminary estimates of relatively good pollen quality (Appendix D), and reports of diploidy in the species studied (Table C-1), it was tentatively assumed that the production of seeds at the McConnell River mainly or wholly involved sexual

Table C-1. Chromosome numbers in the species of Pedicularis studied at the McConnell River

PEDICULARIS	COUNT (2n)	LOCALITY	REFERENCE
flammea L.	16	Iceland	Löve and Löve 1956
	16	Clavering Island and Disko, Greenland	Jørgensen, Sørensen and Westergaard 1958
	16	Scandinavia	Löve and Löve 1948
labradorica Wirsing	16	Ogotoruk Creek, Alaska, U.S.A.	Johnson and Packer 1968
	16	Hasselsfjeld and Sonderstrum, Greenland	Böcher 1967
lapponica L.	16	Disko, Greenland	Jørgensen et al. 1958
	16	TorneTrask, Lappland	Löve and Löve 1944
	16	W. Cukotskij and Pevek, U.S.S.R.	Zhukova 1966
	16	McConnell River, N.W.T., Canada	Mosquin (personal communication)[2]
	16	Chibiny and Kolguijev Island, U.S.S.R.	Sokolovskaja and Strelkova 1960
parviflora Sm. s.l.	16	Shmidt Peninsula, U.S.S.R.	Zhukova 1966
	16	Ogotoruk Creek, Alaska, U.S.A.	Johnson and Packer 1968
sudetica Willd.	16	Ogotoruk Creek, Alaska, U.S.A.	Johnson and Packer 1968
	16	Richardson Mts., Alaska, U.S.A.	Packer 1964
	16	Melville Island, N.W.T., Canada	Mosquin and Hayley 1966
	16	Kolguijev Island and Tiksi Bay, U.S.S.R.	Sokolovskaja and Strelkova 1960
	16	Loveland Pass, Colorado, U.S.A.	Carr 1971

1. Includes Pedicularis pennellii Hult. (see Hultén 1968).
2. Determined by Dr. T. Mosquin, Research Branch, Canada Department of Agriculture, Ottawa.

reproduction. In addition, the absence of seeds in bagged plants of some of the species of Pedicularis indirectly suggests that agamospermy is unlikely to be widespread in those species at the McConnell River. Although a dependence on pollination for seed production could indicate either sexual reproduction or pseudogamy (pollination necessary for seed formation but the embryo is not formed by sexual fusion), it was assumed here to indicate sexual reproduction.

Appendix D

QUALITY AND SIZE OF POLLEN GRAINS

A preliminary examination of pollen was conducted at the McConnell River in 1968 to determine if there was striking morphological evidence of poor pollen quality (i.e. many pollen grains collapsed) and to determine if it was possible to readily identify individual pollen grains of each species. The numbers of observations made in 1968 were limited since electricity for extensive microscope work was not available in the field (light microscope, 400X).

The quality of pollen grains was estimated in pollen samples from one randomly selected flower from each of 8 to 10 plants per species. A second flower was examined in five plants of Pedicularis lapponica to test for consistency of results within a plant. Pollen grains from all the anthers of a flower were mounted in lactophenol (McComb 1968) into which a drop of cotton blue stain had been added. The proportion of stained and uncollapsed (presumably viable) pollen grains out of a total of 200 to 400 pollen grains per flower was recorded.

The sizes of two or more pollen grains from each plant were determined by measuring the maximum diameter of pollen with an ocular micrometer. The largest and smallest pollen grains were selected where possible.

Table D-1. The percentage of stained pollen grains and the range in size of stained pollen grains of Pedicularis at the McConnell River[1].

PEDICULARIS	NUMBER OF PLANTS	PERCENTAGE OF STAINED POLLEN		RANGE IN SIZE OF STAINED POLLEN GRAINS (MICRONS)
		RANGE	MEAN	
parviflora	8	92 - 97	95%	20 - 30
labradorica	8	88 - 97	94%	25 - 27
flammea	8	75 - 98	91%	23 - 28
sudetica	8	72 - 93	83%	20 - 25
lapponica	10	36 - 95	81%	19 - 26

1. Fresh pollen grains were mounted in lactophenol and stained with cotton blue (200 to 400 pollen grains from one flower per plant). Size refers to the maximum diameter of a pollen grain.

The percentage of stained, uncollapsed, pollen averaged over 80% in all species and was over 70% in individual plants of each species except Pedicularis lapponica. (Table D-1). Flowers from seven inflorescences of P. lapponica had greater than 90% stained pollen grains; flowers from three plants had 61%, 58%, and 36% stained pollen grains. Second flowers from each of the latter three plants, plus two of the plants with high percentages of stained pollen grains, had frequencies of stained pollen similar to those found for the first flower (chi square values ranged from 0.002 to 0.61, $P>0.05$). The pollen of most plants, judged from these observations, appeared to be of

relatively good quality.

The level at which pollen quality might become limiting to seed production in plants of Pedicularis lapponica or in plants of the other four species is unknown. Values below 55% stainable pollen in Nigella degenii (Strid 1969) and below 30% in Medicago sativa (Fyfe 1966) have been suggested as limiting seed production in those species.

The pollen grains of the five species showed no differences in size which would permit certain identification of individual pollen grains (Table D-1). No other distinguishing features of the pollen grains could be discerned at the magnification available, although distinguishing features have been described in pollen grains of these and other species of Pedicularis (Erdtman 1952, Tsoong and Chang 1965, Carr 1970).

Appendix E

ROOT HOSTS OF PEDICULARIS

The root systems of 45 randomly selected plants of each species of Pedicularis were examined at the McConnell River during 1966 and 1967. Additional observations of roots, sampled using random coordinates and a somewhat arbitrarily selected starting point, were made at Churchill and at other locations in northern Manitoba (Seal River: 58°49'N, 95°18'W; 59°01'N, 95°47'W; Baralzon Lake, 59°55'N, 98°06'W).

The roots of these samples were examined by removing a 10 by 10 cm plot surrounding a plant of Pedicularis (from 5 to 20 cm deep, depending on the root system) and carefully washing and dissecting the organic material away from the roots. This size of plot included the entire root system of a plant of Pedicularis, except for some plants of P. lapponica where the horizontal spread by rhizomes could not be delimited. I recorded all the species with roots present in the plot and the species whose root systems were attached with the roots of Pedicularis. The shallow depth of the active layer provided excellent conditions for investigations of root systems, since the penetration of roots was limited to the thawed layer. For this study, it was presumed that a haustorium attached to the root of another plant was

functional or had been functional.

Voucher specimens of the host species are available in the herbarium at the University of Western Ontario. Sedges in the genus Carex were generally identified to species in 1967, but noted only by genus in 1966.

First and second year old seedlings from seeds sown into field plots (see Appendix F) were also examined for haustoria at the McConnell River. Plots G3-4 and G3-6 contained first year plants only (year of germination) when examined on 18 August 1967; plots G1 and GE-1 contained both first and second year plants when examined on 19 August 1968.

The results from these two sources are summarized in Tables E-1 and E-2. Ninety-eight percent (284/289) of the naturally occurring plants sampled in 1966 and 1967 at the McConnell River (N.W.T.), at Churchill, and at other locations in northern Manitoba possessed haustoria (Table E-1). The plants of Pedicularis flammea and P. sudetica without haustoria in the year in which they were examined may have had haustoria in previous years (the plants were perennial and the primary roots were no longer present for observation) or they may have developed autotrophically.

Although not all first year (i.e. first growing season) seedlings had haustoria when observations were made in August 1967 or 1968, all the seedlings remaining were apparently hemiparasitic by the end of the second year (Table E-2). If some of the first year seedlings were from

recently germinated seeds, they may have had insufficient time to form haustoria before the observations were made. In other hemiparasites, seedlings may remain free-living for several weeks following germination (e.g. in Orthocarpus spp., Atsatt and Strong 1970). Other factors may also have been unfavorable for the development of haustoria by some seedlings (i.e. the lack of nearby potential host roots). The possession of haustoria by all seedlings which were present from 1967 through August 1968 suggests that plants with haustoria are more likely to survive through a second year than those without haustoria. Unfortunately, it was impossible to ascertain whether these two year old seedlings also had haustoria during their first year (1967).

From these observations, it seems evident that most plants of Pedicularis under field conditions at the McConnell River are hemiparasitic during part of, if not throughout, their adult (post-germination) life. Completion of the adult life without a host (facultative hemiparasitism) might occur very rarely in Pedicularis flammea and P. sudetica; however, because sampling could occur only once in these perennial plants, the lack of hosts at one sampling is insufficient evidence of completely autotrophic development.

Tables E-3 through E-7 list the species of hosts and the frequency with which they were found occurring as hosts of each species of Pedicularis at the McConnell River (based on 45 samples per species of Pedicularis). At the McConnell River, plants of each species of Pedicularis had attachments

on at least 8 to 14 species of hosts from three to seven families. Frequently, single plants were simultaneously attached to more than one species of host. These observations show that these species have relatively broad ranges of hosts, in comparison to host-parasite relationships which might involve only one species, one genus, or even one family. A similar lack of restriction in host species has been found in most other species of Pedicularis which have been examined (Piehl 1965).

Table E-1. The proportion of plants of Pedicularis with haustoria (plants with haustoria/total sample size) from pooled observations made in 1966 and 1967 at the McConnell River and in northern Manitoba.

PEDICULARIS	LOCATIONS					
	MCCONNELL RIVER, N.W.T.		CHURCHILL, MANITOBA		SEAL RIVER AND BARALZON LAKE, MANITOBA	
flammea	43/45	(97%)	11/11	(100%)	--	
labradorica	45/45	(100%)	7/7	(100%)	22/22	(100%)
lapponica	45/45	(100%)	12/12	(100%)	2/2	(100%)
parviflora	45/45	(100%)	--		--	
sudetica	44/45	(98%)	8/10	(80%)	--	

Table E-2. The number of seedlings of Pedicularis with haustoria during the first and second years of growth in field plots at the McConnell River.[1].

PEDICULARIS	PLOT	NUMBER OF SEEDLINGS PRESENT: FIRST YEAR (1967, 1968) TOTAL	WITH HAUSTORIA	(%)	SECOND YEAR (1967 + 1968) TOTAL	WITH HAUSTORIA	(%)
flammea	G1	95	93	(98%)	40	40	(100%)
	G3-4	65	44	(68%)	--	--	--
	G3-6	37	28	(76%)	--	--	--
	GE-1	1	0	(0%)	--	--	--
labradorica	G1	7	4	(57%0	--	--	--
	G3-4	40	19	(47%)	--	--	--
	G3-6	27	6	(22%)	--	--	--
	GE-1	0	--				
lapponica[1].	G1	22	16	(73%)	17	17	(100%)
	GE-1	0	--	--	--	--	--
parviflora[2].	G1	5	3	(60%)	1	1	(100%)
	GE-1	29	21	(72%)	11	11	(100%)
sudetica	G1	0	--	--	--	--	--
	G3-4	0	--	--	--	--	--
	G3-6	0	--	--	--	--	--
	GE-1	2	1	(50%)	16	16	(100%)

1. See Appendix F for details of plots.

2. Species not included in plots G3-4 and G3-6.

Table E-3. The frequency of families and species of plants occurring as hosts of *Pedicularis flammea* at the McConnell River.[1].

HOST FAMILY	HOST SPECIES	NUMBER OF OCCURRENCES AS HOST: TOTAL PER SPECIES	TOTAL PER FAMILY
Cyperaceae	*Carex* spp.[2].	8	
	C. capillaris L.	8	
	C. rariflora (Wahlenb.) Sm.	8	
	C. supina Wahlenb.	8	
	C. misandra R. Br.	6	
	Kobresia simpliciuscula (Wahlenb.) Mack.	4	
	Carex amblyorhyncha Krecz.	3	
	C. rupestris All.	2	
	C. bigelowii Torr.	1	
	C. glacialis Mack.	1	
	C. vaginata Tausch	1	50 (81%)
Ericaceae	*Andromeda polifolia* L.	4	
	Vaccinium uliginosum L.	2	6 (10%)
Juncaceae	*Juncus albescens* (Lange) Fern.	1	
	J. castaneus Smith	1	2 (3%)
Betulaceae	*Betula glandulosa* Michx.	1	1 (<2%)
Equisetaceae	*Equisetum scripoides* Michx.	1	1 (<2%)
Roseceae	*Dryas integrifolia* M. Vahl	1	1 (<2%)
Salicaceae	*Salix* sp.	1	1 (<2%)
		TOTAL:	62 (100%)

1. Based on 45 samples taken in 1966 and 1967.

2. Not identified to species in 1966, except for *Carex supina*.

Table E-4. The frequency of families and species of plants occurring as hosts of *Pedicularis labradorica* at the McConnell River.

HOST		NUMBER OF OCCURRENCES AS HOST	
FAMILY	SPECIES	TOTAL PER SPECIES	TOTAL PER FAMILY
Ericaceae	*Vaccinium vitis-idaea* L. var. *minus* Lodd.	39	
	V. uliginosum L.	13	
	Andromeda polifolia L.	5	
	Arctostaphylos alpina (L.) Spreng.	3	
	Ledum palustre Spreng. var. *decumbens* Ait.	1	61 (94%)
Cyperaceae	*Carex rariflora* (Wahlenb.) Sm.	2	
	C. supina Wahlenb.	1	3 (5%)
Betulaceae	*Betula glandulosa* Michx.	1	1 (1%)
		TOTAL:	65 (100%)

Table E-5. The frequency of families and species of plants occurring as hosts of *Pedicularis lapponica* at the McConnell River.

HOST		NUMBER OF OCCURRENCES AS HOST	
FAMILY	SPECIES	TOTAL PER SPECIES	TOTAL PER FAMILY
Ericaceae	*Vaccinium uliginosum* L.	20	
	Andromeda polifolia L.	15	
	Vaccinium vitis-idaea L. var. *minus* Lodd.	12	
	Rhododendron lapponicum (L.) Wahlenb.	1	48 (79%)
Cyperaceae	*Carex vaginata* Tausch	3	
	C. supina Wahlenb.	2	
	C. saxatilis L.	2	
	Carex spp.	1	8 (13%)
Betulaceae	*Betula glandulosa* Michx.	3	3 (5%)
Salicaceae	*Salix planifolia* Pursh	2	2 (3%)
		TOTAL:	61 (100%)

Table E-6. The frequency of families and species of plants occurring as hosts of *Pedicularis parviflora* at the McConnell River.[1]

HOST FAMILY	HOST SPECIES	NUMBER OF OCCURRENCES AS HOST: TOTAL PER SPECIES	TOTAL PER FAMILY
Cyperaceae	*Carex* spp.[2]	12	
	C. saxatilis L.	9	
	C. stans Drej.	8	
	C. rariflora (Wahlenb.) Sm.	6	
	Kobresia simpliciuscula (Wahlenb.) Mack.	3	
	Carex vaginata Tausch	2	
	C. gynocrates Wormskj.	1	41 (87.2%)
Gramineae	*Arctophila fulva* (Trin.) Anders.	3	3 (6.4%)
Salicaceae	*Salix arctophila* Cock.	3	3 (6.4%)
		TOTAL:	47 (100%)

1. Based on 45 samples taken in 1966 and 1967.

2. Not identified to species in 1966.

Table E-7. The frequency of families and species of plants occurring as hosts of Pedicularis sudetica at the McConnell River.[1]

HOST FAMILY	HOST SPECIES	NUMBER OF OCCURRENCES AS HOST: TOTAL PER SPECIES	TOTAL PER FAMILY
Cyperaceae	Carex spp.[2]	7	
	C. stans Drej.	9	
	C. saxatilis L.	5	
	Kobresia simpliciuscula (Wahlenb.) Mack.	5	
	Carex rariflora (Wahlenb.) Sm.	3	
	C. amblyorhyncha Krecz.	2	
	Scirpus caespitosus L.	2	
	Carex capillaris L.	1	
	C. vaginata Tausch	1	35 (66%)
Gramineae	Poa arctica R. Br.	3	
	Arctophila fulva (Trin.) Anders.	2	5 (9%)
Rosaceae	Potentilla palustris (L.) Scop.	5	5 (9%)
Salicaceae	Salix arctophila Cock.	1	
	S. arctica Pall.	3	4 (8%)
Juncaceae	Juncus albescens (Lange) Fern.	2	2 (4%)
Polygonaceae	Polygonum viviparum L.	2	2 (4%)
		TOTAL:	53 (100%)

1. Based on 45 samples taken in 1966 and 1967.

2. Not identified to species in 1966.

Appendix F

SEED QUALITY AND SEED GERMINATION

The objective of this part of the study was to obtain estimates of the quality, or viability, of the seeds produced by the five species of Pedicularis at the McConnell River. Although seeds of some arctic plants germinate readily in germination tests (cf. Söyrinki 1938-1939, Sørensen 1941, Bliss 1958) and thereby give evidence of their viability, seeds of other species, especially species of Pedicularis, generally fail to germinate (Table F-1). Consequently, in these species whose seeds fail to germinate, it is not known whether the seeds were incapable of germinating or the conditions of the tests (e.g. temperature, moisture, light, duration, handling of the seeds) were inadequate or inappropriate. Because of the lack of information on conditions which would promote germination and hence give some indication of viability of seeds of these species of Pedicularis, most of the seeds which could be collected at the McConnell River were sown into field plots and estimates of the seed quality of a species were based on the highest percentage of germination found in any of the field plots. Some of the seeds collected in 1965 were tested in the laboratory (University of Western Ontario) using treatments known to promote germination in

Table F-1. Reported attempts to germinate the seeds of *Pedicularis flammea*, *P. labradorica* and *P. lapponica*.

PEDICULARIS	CONDITIONS OF TEST	GERMINATION	AUTHOR
flammea	unknown quantity of seeds from Eskimonoas, West Greenland; stored at room temperature; tested in filter paper cones on damp soil in the field (May - July)	+	Sørensen 1941
labradorica	109 seeds from Umiat, Alaska; stored 6-7 months at -15 C; tested in constant temperature (22 C) and constant light or dark	0	Bliss 1958
lapponica	(same as *P. flammea* above)	0	Sørensen 1941
	100 seeds from Petsamo-Lappland; exposed to freezing temperatures; tested under varying temperatures and light-dark conditions	0	Söyrinki 1938-1939
	50 seeds from Petsamo-Lappland; exposed to freezing temperatures; tested outside in soil at botanical garden	12%	Söyrinki 1938-1939

other species of plants (e.g. scarification of the seed coat, application of gibberellic acid, cf. Mayer and Poljakoff-Mayber 1963).

The field plots for the germination tests at the McConnell River were arbitrarily located in areas with and without plants of the various species of Pedicularis present: the plots included areas where seeds of Pedicularis had germinated previously, areas into which seeds were likely to be shed by the plants present, and other areas which may or may not have possessed conditions favorable for germination. The object here was to test the seeds under a range of field conditions; the conditions within each of the plots, or quadrats within the plots, were not studied here.

The plots consisted of groups of 5 by 5 cm quadrats; some quadrats were sown with seeds of Pedicularis (50 seeds per quadrat) and others were left without seeds (control). Each quadrat was surrounded by 10 cm of border. Seeds of each species of Pedicularis used in a particular plot were sown into three to six quadrats per plot; the quadrats sown with seeds were randomly selected. The capsules of naturally occurring plants of Pedicularis within the plots were removed from the plants before their seeds were shed.

Three sets of plots (G1, G2, and G3) were established on 20 July, 1966, using seeds collected in August 1965 within a few days of the first observed capsule dehiscence of each species of Pedicularis. These seeds were stored in paper

bags in an unheated building in the nearby settlement of Eskimo Point during the winter of 1965-1966, and then taken back to the McConnell River for sowing in July 1966. The seed collections for each species were pooled and mixed before the seeds were counted. Plots in set G1 included five species of Pedicularis; plots in set G2, two species; plots in set G3, three species. Three additional plots (GE-1, GE-2, GE-3) were established on 15 August, 1966, using seeds of all five species collected between 29 July and 11 August (1966) as their fruits ripened.

The numbers of germinated seeds (indicated by the presence of cotyledon leaves) were recorded at two to four week intervals during July and August in 1966, 1967, and 1968, depending on when the plots were established. No data were obtained from plot GE-3: the markers indicating its location were missing in 1967. The amount of germination is expressed here as a percentage of the seeds sown. Since some of the seeds may have disappeared from the quadrats during the study, the percentage of germination recorded here may underestimate the percentage of germination based on the number of seeds actually present. There was no evidence of an input of additional seeds giving rise to seedlings in either the control quadrats or the border areas.

The numbers of germinated seeds are listed by plot where the plot included all five species of Pedicularis (Table F-2, plot G1 with 1965 seeds; Table F-3, plot GE-1 with 1966 seeds) and by species when less than five species

were sown in the plots (Tables F-4 to F-7, plots in sets G2 and G3 with 1965 seeds). The results for plot GE-2 were not put in a table: no germinated seeds of any of the five species were found.

The data in these tables show the variability in germination among the quadrats within a plot (within a species), among the plots (within a species and year of seed production), and among species. For example, from 8% to 84% of the seeds (1965) of Pedicularis flammea sown in quadrats of plot G1 germinated (Table F-2), from 0% to 2% of the seeds (1966) of P. flammea sown in quadrats of plot GE-1 germinated (Table F-3) and from 0% to 70% of the seeds (1965) of P. flammea sown in the quadrats and plots of set G3 germinated (Table F-4).

Thus, under a variety of field conditions over several years, the maximum estimation of germination from 1965 produced seeds of Pedicularis flammea was 84%. This suggests that its seed quality was relatively high in 1965. Presumably fewer seeds germinated in other quadrats because the conditions associated with those quadrats were less favorable or because more seeds were lost from the quadrats or both. In contrast, the highest percentage germination recorded from 1966 seeds of P. flammea was 2%; unfortunately there is no way of knowing whether this indicated that the seeds were poor in quality. None of the other species of Pedicularis had as high a percentage germination in the

field tests as P. flammea (using either 1965 or 1966 seeds, see summary in Table F-8).

Some of the seeds collected at the McConnell River in August 1965 were stored for approximately six months at -10 C and then used in preliminary germination tests conducted between 20 March and 20 May at the University of Western Ontario. The treatments, all conducted under alternating light and temperature conditions (20 hours light at 22 C, 4 hours dark at 7 C), included scarification of the seed coat (with a needle) and the application of gibberellic acid (GA_3, 20 ml of 1.0×10^{-3} M; cf. Mayer and Poljakoff-Mayber 1963). The highest percentages of germination obtained within any of the treatments, including a gibberellic acid treatment similar to one which induced an average of 97% germination in Pedicularis parryi (McDonough 1969), were all lower than those found in the field and therefore gave less positive information on seed viability than the field tests cited here.

Table F-2. The number of germinated seeds of five species of Pedicularis appearing in field plot G1 in 1967 and 1968 (McConnell River).[1].

PEDICULARIS	YEAR	GERMINATED SEEDS APPEARING IN QUADRATS						ANNUAL TOTAL	TOTAL 1968	TOTAL SEEDS SOWN	AVERAGE PERCENTAGE GERMINATION
flammea	1967	2	19	5	10	15	2	53			
	1968	22	23	22	6	20	2	95			
	total	24	42	27	16	35	4		148	300	49%
labradorica	1967	0	0	0	0	0	0	0			
	1968	1	2	1	5	2	3	14			
	total	1	2	1	5	2	3		14	300	5%
lapponica	1967	3	1	8	7	4	3	26			
	1968	1	4	3	10	5	1	24			
	total	4	5	11	17	9	4		50	300	17%
parviflora	1967	2	2	2	2	0	3	11			
	1968	2	1	3	2	3	4	15			
	total	4	3	5	4	3	7		26	300	9%
sudetica	1967	0	0	0	0	0	0	0			
	1968	0	0	0	3	0	0	3			
	total	0	0	0	3	0	0		3	300	1%

1. See text for methods (1965 seeds).

Table F-3. The number of germinated seeds of five species of Pedicularis appearing in field plot GE-1 in 1967 and 1968.[1].

PEDICULARIS	YEAR	GERMINATED SEEDS APPEARING IN QUADRATS						ANNUAL TOTAL	TOTAL 1968	TOTAL SEEDS SOWN	AVERAGE PERCENTAGE GERMINATION
flammea	1967	0	1	0	0	0	0	1			
	1968	1	0	0	0	0	0	1			
	total	1	1	0	0	0	0		2	300	1%
labradorica	1967	1	6	0	6	0	1	14			
	1968	0	0	0	0	0	0	0			
	total	1	6	0	6	0	1		14	300	5%
lapponica	1967	0	2	3	4	0	1	10			
	1968	0	0	0	0	0	0	0			
	total	0	2	3	4	0	1		10	300	3%
parviflora	1967	6	9	22	4	3	4	48			
	1968	12	7	4	2	4	3	32			
	total	18	16	26	6	7	7		80	300	27%
sudetica	1967	2	5	3	5	1	5	21			
	1968	0	0	0	0	0	2	2			
	total	2	5	3	5	1	7		23	300	8%

1. See text for methods (1966 seeds).

Table F-4. The number of germinated seeds of Pedicularis flammea appearing in field plots, set G3, in 1967 or 1967 and 1968.

PLOT	YEAR	GERMINATED SEEDS APPEARING IN QUADRATS					ANNUAL TOTAL	TOTAL 1968	TOTAL SEEDS SOWN	AVERAGE PERCENTAGE GERMINATION
1	1967	6	8	20	19	11	64			
	1968	7	18	14	14	19	72			
	total	13	26	34	33	30		136	250	54%
2	1967	22	23	30	30	21	126			
	1968	3	6	5	4	0	18			
	total	25	29	35	34	21		144	250	58%
3	1967	21	7	20	19	10	77			
	1968	12	1	0	0	0	13			
	total	33	8	20	19	10		90	250	36%
4[1]	1967	27	13	5	0	0	45			
	--	-	-	-	-	-	-	-	250	-
5	1967	1	23	25	20	7	76			
	1968	0	5	8	10	2	25			
	total	1	28	33	30	9		101	250	40%
6[1]	1967	16	18	8	10	26	78			
	--	-	-	-	-	-	-	-	250	-
7	1967	0	4	24	1	12	41			
	1968	0	0	4	0	0	4			
	total	0	4	28	1	12		45	250	18%

1. Seedlings were removed from examination on 14 August,1967.

Table F-5. The number of germinated seeds of Pedicularis labradorica appearing in field plots, set G3, in 1967 or 1967 and 1968.

PLOT	YEAR	GERMINATED SEEDS APPEARING IN QUADRATS					ANNUAL TOTAL	TOTAL 1968	TOTAL SEEDS SOWN	AVERAGE PERCENTAGE GERMINATION
1	1967	0	0	0	0	4	4			
	1968	7	18	16	24	23	88			
	total	7	18	16	24	27		92	250	37%
2	1967	12	11	20	16	14	73			
	1968	6	15	2	0	1	24			
	total	18	26	22	16	15		97	250	39%
3	1967	22	0	13	0	20	55			
	1968	0	0	0	0	3	3			
	total	22	0	13	0	23		58	250	23%
4[1]	1967	16	6	5	1	2	30			
		-	-	-	-	-	-	-	250	-
5	1967	11	10	1	5	14	41			
	1968	5	8	0	9	1	23			
		16	18	1	14	15		64	250	26%
6[1]	1967	7	14	5	8	12	46			
		-	-	-	-	-	-	-	250	-
7	1967	0	9	11	1	0	21			
	1968	0	1	4	0	0	5			
		0	10	15	1	0		26	250	10%

1. Seedlings were removed for examination on 14 August, 1967.

Table F-6. The number of germinated seeds of Pedicularis sudetica appearing in field plots, set G3, in 1967 or 1967 and 1968.

PLOT	YEAR	GERMINATED SEEDS APPEARING IN QUADRATS					ANNUAL TOTAL	TOTAL 1968	TOTAL SEEDS SOWN	AVERAGE PERCENTAGE GERMINATION
1	1967	0	0	0	0	0	0			
	1968	0	0	0	2	0	2			
	total	0	0	0	2	0		2	250	1%
2	1967	2	1	0	0	2	5			
	1968	0	0	0	0	0	0			
	total	2	1	0	0	2		5	250	2%
3	1967	0	0	0	1	0	1			
	1968	0	0	0	0	0	0			
	total	0	0	0	1	0		1	250	0.5%
4[1].	1967	0	0	1	1	0	2			
	-	-	-	-	-	-	-	-	250	-
5	1967	0	0	0	0	2	2			
	1968	0	0	0	0	0	0			
	total	0	0	0	0	2		2	250	1%
6[1].	1967	0	0	0	1	0	1			
	-	-	-	-	-	-	-	-	250	-
7	1967	0	0	0	0	0	0			
	1968	0	0	0	0	0	0			
	total	0	0	0	0	0		0	250	0%

1. Seedlings were removed for examination on 14 August, 1967.

Table F-7. The number of germinated seeds of Pedicularis parviflora and P. sudetica appearing in field plots, set G2, in 1967 or 1967 and 1968.

PLOT	PEDICULARIS	YEAR	GERMINATED SEEDS APPEARING IN QUADRATS			ANNUAL TOTAL	TOTAL 1968	TOTAL SEEDS SOWN	AVERAGE PERCENTAGE GERMINATION
1[1].	parviflora	1967	0	0	0	0	-	150	0%
	sudetica	1967	0	0	0	0	-	150	0%
2[1].	parviflora	1967	0	0	0	0	-	150	0%
	sudetica	1967	0	0	0	0	-	150	0%
3[1].	parviflora	1967	0	0	0	0	-	150	0%
	sudetica	1967	0	0	0	0	-	150	0%
4[1].	parviflora	1967	0	0	0	0	-	150	0%
	sudetica	1967	0	0	0	0	-	150	0%
5	parviflora	1967	0	0	0	0			
		1968	0	2	1	3			
		total	0	2	1		3	150	2%
	sudetica	1967	0	0	0	0			
		1968	0	0	0	0	0	150	0%
6	parviflora	1967	0	0	0	0			
		1968	0	1	0	1			
		total	0	1	0		1	150	1%
	sudetica	1967	0	0	0	0			
		1968	0	0	0	0	0	150	0%

1. Seedlings were removed for examination on 14 August, 1967.

Table F-8. A summary of field germination tests using seeds of Pedicularis produced in 1965 and 1966 at the McConnell River.[1]

PEDICULARIS	SEEDS PRODUCED	NUMBER OF QUADRATS	TOTAL SEEDS SOWN	RANGE IN PERCENTAGE GERMINATION IN INDIVIDUAL QUADRATS
flammea	1965	31	1550	0 - 84%
	1966	12	600	0 - 2%
labradorica	1965	31	1550	0 - 54%
	1966	12	600	0 - 12%
lapponica	1965	6	300	8 - 34%
	1966	12	600	0 - 8%
parviflora	1965	12	600	0 - 14%
	1966	12	600	0 - 52%
sudetica	1965	37	1850	0 - 6%
	1966	12	600	0 - 14%

1. This data, summarized from Tables F-2 through F-7 but excluding the quadrats observed in 1967 only, gives the total percentage germination found by August 1968.

REFERENCES

Allard, R. W. 1965. Genetic systems associated with colonizing ability in predominantly self-pollinated species, p. 49-75. In H. G. Baker and G. L. Stebbins (eds.), Genetics of colonizing species. Academic Press, New York.

Anderson, J. P. 1959. Flora of Alaska and adjacent parts of Canada. Iowa State University Press, Ames, Iowa. 534 p.

Andrews, J. T. 1969. The pattern and interpretation of restrained, post-glacial and residual rebound in the area of Hudson Bay, p. 49-62. In P. J. Hood (ed.), Earth science symposium on Hudson Bay. Geological Survey of Canada Paper 68-53.

Antonovics, J. 1968. Evolution of closely adjacent plant populations V. Evolution of self-fertility. Heredity 23: 219-238.

Atsatt, P. R. 1970. Hemiparasitic flowering plants: phenotypic canalization by hosts. Nature 225: 1161-1163.

_____ and D. R. Strong. 1970. The population biology of annual grassland hemiparasites I. The host environment. Evolution 24: 278-291.

Aurivillius, C. 1883. Insect life in arctic lands, p. 403-459. In A. E. Nordenskiold, Studier och forskningar föranledda af mina resor i höga norden. (Trans. S. Nimmo 1970, ed. P. Kevan, Boreal Institute, University of Alberta, Edmonton, Alberta, Canada) F. & B. Beijers Forlag, Stockholm.

Barnett, D. M. 1966. A re-examination and re-interpretation of tide gauge data for Churchill, Manitoba. Canadian Journal of Earth Science 3: 77-88.

Beckel, D. K. Brown. 1957. Studies on seasonal changes in the temperature gradient of the active layer of soil at Fort Churchill, Manitoba. Arctic 10: 151-183.

Bennett, B. M. and C. Horst, 1966. Supplement to tables for testing significance in a 2 x 2 contingency table. Cambridge University Press, Cambridge. 28 p.

Berg, R. Y. 1954. Development and dispersal of the seed of Pedicularis sylvatica. Nytt Magasin für Botanikk 2: 1-60.

Beschel, R. E. 1970. The diversity of tundra vegetation, p. 85-92. In W. A. Fuller and P. G. Kevan (eds.), Productivity and conservation in Northern Circumpolar Lands. IUCN Publications New Series Number 16.

Billings, W. D. and H. A. Mooney. 1968. The ecology of arctic and alpine plants. Biological Reviews 43: 481-529.

Bird, J. B. 1967. The physiography of arctic Canada. The Johns Hopkins Press, Baltimore, Maryland. 336 p.

Bliss, L. C. 1958. Seed germination in arctic and alpine species. Arctic 11: 180-188.

_____ 1962. Adaptations of arctic and alpine plants to environmental conditions. Arctic 15: 117-144.

Böcher, T. W. 1952. Contribution to the flora and plant geography of West Greenland. III. Meddelelser om Grønland 147: 1-85.

_____ 1967. IOBP chromosome number reports. Taxon 11: 215-222.

_____, K. Holmen and K. Jakobsen. 1968. The flora of Greenland. P. Haase & Son, Copenhagen. 312 p. (T. T. Elkington & M. C. Lewis, Translators).

Boeshore, I. 1920. The morphological continuity of Scrophulariaceae and Orobanchaceae. Contributions of the Botanical Laboratory, University of Pennsylvania 5: 139-177.

Brassard, G. R. and R. E. Beschel. 1968. The vascular flora of Tanquary Fiord, northern Ellesmere Island, N.W.T. Canadian Field-Naturalist 82: 103-113.

Breedlove, D. E. and P. R. Ehrlich. 1968. Plant-herbivore co-evolution: lupines and lycaenids. Science 162: 671-672.

Breese, E. L. 1959. Selection for differing degrees of out-breeding in Nicotiana rustica. Annals of Botany, New Series, 23 (90): 331-344.

Britton, M. E. 1966. Vegetation of the arctic tundra. Oregon State University Press, Oregon. 64 p.

Brown, R. J. E. 1960. The distribution of permafrost and its relation to air temperature in Canada and the USSR. Arctic 13: 163-177.

Bryson, R. A. 1966. Air masses, streamlines, and the boreal forest. Geographical Bulletin 8: 228-269.

Cantlon, J. E. 1969. The stability of natural populations and their sensitivity to technology, p. 197-205. In Diversity and stability in ecological systems. Brookhaven Symposia in Biology Number 22. Brookhaven National Laboratory, Upton, New York.

Carr, G. W. 1970. Systematic biology of Pedicularis parryi (Scrophulariaceae) with notes on P. sudetica, P. cystopteridifolia, and associated species. Unpublished M. S. thesis. University of Wisconsin-Milwaukee. 87 p.

_____ 1971. IOPB chromosome number reports. Taxon 20: 157-160.

Cheney, T. A. and D. K. Brown Beckel. 1955. Fort Churchill environmental analysis. Cornell University, Ithaca, New York. 349 p.

Cody, W. J. 1965. Plants of the Mackenzie River Delta and Reindeer Grazing Preserve. Canada Department of Agriculture, Plant Research Institute. 56 p.

_____ and A. E. Porsild. 1968. Additions to the flora of continental Northwest Territories, Canada. Canadian Field-Naturalist 82: 263-275.

Connor, H. E. 1966. Breeding systems in New Zealand grasses. VII. Periodic flowering of snow tussock, Chionochloa rigida. New Zealand Journal of Botany 4: 392-397.

Craig, B. C. 1969. Late-glacial and postglacial history of the Hudson Bay region, p. 63-77. In P. J. Hood (ed.), Earth science symposium on Hudson Bay. Geological Survey of Canada Paper 68-53.

Curran, C. H. and C. L. Fluke. 1926. Revision of the neartic species of Helophilus and allied genera. Wisconsin Academy of Science, Transactions 22: 207-281.

Day, J. H. 1964. Characteristics of the soils of Hazen Camp area, northern Ellesmere Island, N.W.T. Defence Research Board, Directorate of Physical Research (G), Ottawa. Hazen 24. 15 p.

DeBach, P. 1964. Biological control of insect pests and weeds. Reinhold, New York. 844 p.

Downes, J. A. 1964. Arctic insects and their environment. Canadian Entomologist 96: 279-307.

_____ 1965. Adaptations of insects in the arctic. Annual Review of Entomology 10: 257-274.

Dunbar, M. J. 1968. Ecological development in polar regions. Prentice-Hall, Inc., Englewood Cliffs, New Jersey. 119 p.

Erdtman, G. 1952. Pollen morphology and plant taxonomy. Angiosperms. Chronica Botanica, Waltham, Massachusetts. 514 p.

Faegri, K. and L. van der Pijl. 1966. The principles of pollination ecology. Pergamon Press, New York. 248 p.

Filion, W. G. 1970. Cytogenetic analysis of addition segments in the short arm of chromosome 9 in Zea mays L.

Unpublished Ph. D. thesis, Department of Botany, University of Western Ontario, London. 242 p.

Finney, D. J., R. Latscha, B. M. Bennett and P. Hsu. 1963. Tables for testing significance in a 2 x 2 contingency table. Cambridge University Press, Cambridge. 103 p.

Fyfe, J. L. 1966. The reproductive biology of some leguminous crops, p. 40-50. In J. G. Hawkes (ed.), Reproductive biology and taxonomy of vascular plants. Pergamon Press, London.

Gilmour, J. S. J. and J. W. Gregor. 1939. Demes: a suggested new terminology. Nature 144: 333.

Govier, R. N. 1966. The inter-relationships of the hemi-parasites and their hosts, with special reference to Odontites verna (Bell.) Dum. Unpublished Ph.D. thesis. University of Wales, Bangor. 92 p.

_____, M. D. Nelson, and J. S. Pate. 1967. Hemi-parasitic nutrition in angiosperms I. The transfer of organic compounds from host to Odontites verna (Bell.) Dum. (Scrophulariaceae). New Phytologist 66: 285-297.

Griffiths, G. C. D. 1968. Agromyzidae (Diptera) from Ireland. Proceedings of the Royal Irish Academy 67, B(2): 37-61.

Gustafsson, Å. 1946-1947. Apomixis in higher plants. Lunds Universitets Årsskrift 42-43: 1-370.

Harper, J. L. 1967. A Darwinian approach to plant ecology. Journal of Ecology 55: 247-269.

_____ and J. Ogden. 1970. The reproductive strategy of higher plants: I. The concept of strategy with special reference to Senecio vulgaris. Journal of Ecology 58: 681-698.

Harris, P. 1963. Host specificity of Calophasia lunula (Hufn.) (Lepidoptera: Noctuidae). Canadian Entomologist 95: 101-105.

Hering, E. M. 1949. Die Phytomyza-Arten von Pedicularis (Dipt. Agromyz.) Entomon 1: 182-183.

Hicks, D. R. and J. W. Pendleton. 1969. Effect of floral bud removal on performanee of soybeans. Crop Science 9: 435-437.

Hillman, W. S. 1962. The physiology of flowering. Holt, Rinehart and Winston, New York. 164 p.

Hocking, B. 1968. Insect-flower associations in the high arctic with special reference to nectar. Oikos 19: 359-388.

Høeg, O. A. 1924. Pollen of bumblebees from Novaya Zemlya. Report of Norwegian Expedition to Novaya Zemlya. Number 27: 3-18.

Holttum, R. E. 1922. The vegetation of West Greenland. Journal of Ecology 10: 87-108.

Huffaker, C. B. 1959. Biological control of weeds with insects. Annual Review of Entomology 4: 251-276.

Hultén, E. 1941-1950. Flora of Alaska and Yukon, Parts I-X. Lunds Universitets Arsskrift, N. F. Volumes 37-46.

_____ 1961. Two Pedicularis species from northwest America, P. albertae n. sp. and P. sudetica sens. lat. Svensk Botanisk Tidskrift 55: 193-204.

_____ 1964. Pedicularis sudetica in Colorado. Svensk Botanisk Tidskrift 58: 435-437.

_____ 1968. Flora of Alaska and neighboring territories. Stanford University Press, Stanford, California. 1008 p.

Jain, S. K., D. R. Marshall and K. Wu. 1970. Genetic variability in natural populations of softchess (Bromus mollis L.) Evolution 24: 649-659.

Janzen, D. H. 1967. Interaction of the bull's horn acacia (Acacia cornigera L.) with an ant inhabitant (Pseudomyrmes ferruginea F. Smith) in eastern Mexico. Kansas University Science Bulletin 47: 315-558.

_____ 1969. Seed-eaters versus seed size, number, toxicity and dispersal. Evolution 23: 1-27.

_____ 1970. Herbivores and the number of tree species in tropical forests. American Naturalist 104: 501-528.

Johnson, A. W. and J. G. Packer. 1968. Chromosome numbers in the flora of Ogotoruk Creek, N. W. Alaska. Botaniska Notiser 121: 403-456.

Johnson, M. P. and S. A. Cook. 1968. "Clutch size" in buttercups. American Naturalist 102: 405-411.

Jørgensen, C. A., T. Sørensen and M. Westergaard. 1958. The flowering plants of Greenland. A taxonomical and cytological survey. Biologiske Skrifter udgivet of Det Kongelige Danske Videnskabernes Selskab 9(4): 1-172.

Kannenberg, L. W. and R. W. Allard. 1967. Population studies in predominantly self-pollinated species. VIII. Genetic variability in the Festuca microstacys complex. Evolution 21: 227-240.

Kelsall, J. P. 1968. The migratory barren-ground caribou of Canada. Canadian Wildlife Service Monograph 3. 340 p.

Kerner, A. 1894-1895. The natural history of plants, their forms, growth, reproduction and distribution. Trans. F. W. Oliver, Henry Holt and Co., New York. I: 777 p., II: 983 p.

Kevan, P. G. 1970. High arctic insect-flower relations: the inter-relationships of arthropods and flowers at Lake Hazen, Ellesmere Island, Northwest Territories, Canada. Unpublished Ph.D. thesis, Dept. of Entomology, University of Alberta, Edmonton. 399 p.

Klebesadel, L. J. 1971. Native Alaskan legumes studied. Agroborealis 3: 9-11.

Koyama, H. and T. Kira. 1956. Intraspecific competition among higher plants. VIII. Frequency distribution of individual plant weight as affected by the interaction between plants. Osaka City University, Institute of Polytechnics, D. Journal of Biology 7: 73-94.

Knuth, P. 1906-1909. Handbook of flower pollination. Vols. I-III. Trans. by J. R. Ainsworth, Davis. Clarendon Press, Oxford. 382 p., 703 p., 644 p. (Translation of Bde. I-II of German Edition).

Kuijt, J. 1969. The biology of parasitic flowering plants. University of California Press, Berkeley. 246 p.

Lagerberg, T., J. Holmboe and R. Nordhagen. 1957. Våre ville planter. VI. 1: 139-172.

Lange, J. 1870-1871. Bemaefkninger om frøenes form og skulptur hos beslektede arter i forskjellige slekter. Botanisk Tidsskrift 4: 230-271.

Lee, H. A. 1959. Surficial geology of southern District of Keewatin and the Keewatin ice divide, Northwest Territories. Geological Survey of Canada. Bulletin 51. 42 p.

_____ 1968. Quaternary geology, p. 503-543. In C. S. Beals (ed.), Science, history and Hudson Bay, Volume 2. Queen's Printer, Ottawa.

Li, H-L. 1951. Evolution in the flowers of Pedicularis. Evolution 5: 158-164.

Linck, A. J. 1961. The morphological development of the fruit of Pisum sativum var. Alaska. Phytomorphology 2: 79-84.

Lord, C. S. 1953. Geological notes on southern District of Keewatin, Northwest Territories. Geological Survey of Canada, Paper 53-22. 11 p.

Löve, A. and D. Löve. 1944. Cytotaxonomical studies on boreal plants. III. Some new chromosome numbers of Scandinavian plants. Arvik for Botanik 31 A, 12: 1-23.

_____ 1948. Chromosome numbers of northern plant species. Iceland University Institute of Applied Sciences, Department of Agriculture Reports, Series B. Number 3. 131 p.

_____ 1956. Cytotaxonomical conspectus of the Icelandic flora. Acta Horti Gotoburgensis 20: 65-290.

Löve, D. 1970. Subarctic and subalpine: where and what? Arctic and Alpine Research 2: 63-73.

Lyons, L. A. 1956. The seed production capacity and efficiency of red pine cones (Pinus resinosa Ait.). Canadian Journal of Botany 34: 27-36.

Macior, L. W. 1968a. Pollination adaptation in Pedicularis groenlandica. American Journal of Botany 55: 927-932.

_____ 1968b. Pollination adaptation in Pedicularis canadensis. American Journal of Botany 55: 1031-1035.

_____ 1969. Pollination adaptation in Pedicularis lanceolata. American Journal of Botany 56: 853-859.

_____ 1970. The pollination ecology of Pedicularis in Colorado. American Journal of Botany 57: 716-728.

Manning, A. 1956. Some aspects of the foraging behavior of bumblebees. Behaviour 9: 164-302.

Mark, A. F. 1965. Flowering, seeding, and seedling establishment of narrow-leaved snow tussock, Chionochloa rigida. New Zealand Journal of Botany 3: 180-193.

_____ 1968. Factors controlling irregular flowering in four alpine species of Chionochloa. Proceedings of the New Zealand Ecological Society 15: 55-60.

Mathiesen, Fr. J. 1921. The structure and biology of arctic flowering plants. II. 15. Scrophulariaceae. Meddelelser om Grønland 37: 358-507.

Maybrook, A. C. 1917. On the haustoria of Pedicularis vulgaris Tournef. Annals of Botany 31: 499-511.

Mayer, A. M. and A. Poljakoff-Mayber. 1963. The germination of seeds. Macmillan and Co., New York. 236 p.

McAlister, D. F. and O. A. Krober. 1958. Response of soybeans to leaf and pod removal. Agronomy Journal 50: 674-677.

McComb, J. A. 1968. The occurrence of unisexuality and polyploidy in Isotoma fluviatilis. Australian Journal of Botany 16: 525-537.

McDonough, W. T. 1969. Effective treatments for the induction of germination in mountain rangeland species. Northwest Science 43: 18-22.

Meteorological Branch, Canada Department of Transport. 1965a. Temperature normals for Manitoba. CDS 2-65. 5 p.

_____ 1965b. Precipitation normals for Manitoba. CDS 7-65. 5 p.

_____ 1965c. Precipitation normals for the Yukon and Northwest Territories. CDS 12-65. 7 p.

Molisch, H. 1938. The longevity of plants (Die Lebensdauer der Pflanze). Trans. by E. H. Fulling. The Science Pressing Printing Co., Lancaster, Pennsylvania. 226 p.

Moore, D. M. and H. Lewis. 1965. The evolution of self-pollination in Clarkia xantiana. Evolution 19: 104-114.

Mosquin, T. 1966. Reproductive specialization as a factor in the evolution of the Canadian flora, p. 43-65. In R. L. Taylor and T. A. Ludwig (eds.), The evolution of Canada's flora. University of Toronto Press, Toronto.

_____ and D. E. Hayley. 1966. Chromosome numbers and taxonomy of some Canadian plants. Canadian Journal of Botany 44: 1209-1217.

_____ and J. E. H. Martin. 1967. Observations on the pollination biology of plants on Melville Island, N.W.T., Canada. Canadian Field-Naturalist 81: 201-205.

Müller, H. 1884. The fertilization of flowers by insects. Trans. and edited by D. W. Tompson. Macmillan and Co., London. 669 p.

Neff, S. E. 1968. Observations on the immature stages of Gimnomera cerea and G. incisurata (Diptera: Anthomyiidae, Scatophaginae). Canadian Entomologist 100: 74-83.

Obied, M., D. Machin and J. L. Harper. 1967. Influence of density on plant variation in fiber flax, Linum usitatissium L. Crop Science 7: 471-473.

Orndduff, R. 1969. Reproductive biology in relation to systematics. Taxon 18: 121-133.

Packer, J. C. 1964. Chromosome numbers and taxonomic notes on western Canadian and arctic plants. Canadian Journal of Botany: 42: 473-494.

Pedersen, M. W. 1953. Environmental factors affecting nectar secretion and seed production in alfalfa. Agronomy Journal 45: 359-361.

Peterken, G. F. 1967. Guide to the check-sheet for IBP areas. Blackwell Scientific Publications. Oxford. 133 p.

Piehl, M. A. 1963. Mode of attachment, haustorium structure, and hosts of Pedicularis canadensis. American Journal of Botany 50: 978-985.

_____ 1965. Studies of root parasitism in Pedicularis lanceolata. The Michigan Botanist 4: 75-81.

Polunin, N. 1951. The real arctic: suggestions for its delineation, subdivision, and characterization. Journal of Ecology 39: 308-315.

_____ 1959. Circumpolar arctic flora. Oxford University Press, Oxford. 514 p.

Porsild, A. E. 1951a. Plant life in the arctic. Canadian Geographical Journal 42: 120-145.

_____ 1951b. Botany of Southeastern Yukon adjacent to the Canol Road. National Museum of Canada Bulletin 121: 1-400.

_____ 1964. Illustrated flora of the Canadian Arctic Archipelago. National Museum of Canada Bulletin 146, 2nd ed., 218 p.

Porsild, M. P. 1920. Flora of Disko Island and West Greenland, from 66° - 71°N latitude. With remarks on phytogeography, ecology, flowering, fructification, and hibernation. Meddelelser om Grønland 58: 1-156.

Robotnov, R. A. 1960. Some problems in increasing the proportion of leguminous species in permanent meadows, p. 260-264. In Proceedings of the 8th International Grassland Congress, Reading.

_____ 1969. On coenopopulations of perennial herbaceous plants in natural coenoses. Vegetatio 19: 87-95.

Raup, H. M. 1947. The botany of southwestern Mackenzie. Sargentia 6: 1-275.

Resvoll, T. 1917. Om planter somm passer til kort og kold sommer. Archiv for Mathematic og Naturvidenskab Bd. 35: 1-219.

Richards, K. W. 1970. Biological studies of arctic bumble-bees. Unpublished M. Sc. thesis, Dept. of Entomology, University of Alberta, Edmonton. 165 p.

Richards, O. W. 1927. Some notes on the humble-bees allied to Bombus alpinus L. Tormso Museums Arshefter 50: 1-32.

Ritchie, J. C. 1956. The native plants of Churchill, Manitoba. Canadian Journal of Botany 34: 269-320.

_____ 1957. The vegetation of northern Manitoba. II. A prisere on the Hudson Bay Lowlands. Ecology 38: 429-435.

Rochow, T. F. 1970. Ecological investigations of Thlaspi alpestre L. along an elevational gradient in the central Rocky Mountains. Ecology 51: 649-656.

Rowlands, D. G. 1960. Fertility studies in the field bean (Vicia faba L.). I. Cross- and self-fertility. Heredity 15: 497-508.

Rydberg, P. A. 1932. Flora of the prairies and plains of central North America. The New York Botanical Garden, New York. 969 p.

Rydén, N. 1956. Zur Kenntnis schwedischer Minierer XVIII. Opuscula Entomologica 21: 191-200.

Salisbury, E. J. 1942. The reproductive capacity of plants. G. Bell and Sons, London. 244 p.

Savile, D. B. O. 1959. The botany of Somerset Island, District of Franklin. Canadian Journal of Botany 37: 959-1002.

_____ 1966. Unity from diversity in biological research. Transactions of the Royal Society of Canada. Volume IV, Series IV, Section III: 245-251.

_____ 1972. Arctic adaptations in plants. Canada Department of Agriculture Monograph 6. 81 p.

Scoggan, H. J. 1957. Flora of Manitoba. National Museum of Canada Bulletin Number 140. 619 p.

Shamurin, V. F. 1966. Seasonal rhythm and ecology of flowering of plants in the tundra communities of northern Yakutia, p. 5-125. In B. A. Tikhomirov, Rasti tel'nost krainege severa SSSR i ee osboenie, vyp. 8, Prisposoblenie rastenii Arktitik usloviiam sredy. Moscow.

Singer, M. C. 1971. Evolution of food-plant preferences in the butterfly Euphydryas editha. Evolution 25: 383-389.

Smith, B. W. 1954. Arachis hypogea, reproductive efficiency. American Journal of Botany 41: 607-616.

Snedecor, G. W. and W. G. Cochran. 1967. Statistical methods. 6th ed., Iowa State University Press. Ames, Iowa. 593 p.

Sokal, R. R. and F. J. Rohlf. 1969. Biometry. W. H. Freeman and Co., San Francisco, California. 776 p.

Sokolovskaja, A. P. and O. S. Strelkova. 1960. Geographical distribution of the polyploid species of plants in the Eurasiatic Arctic. Botanicheskii Zhurnal 45: 369-381.

Sørensen, T. 1941. Temperature relations and phenology of the northeast Greenland flowering plants. Meddelelser om Grønland 125: 1-305.

Söyrinki, N. 1938-1939. Studien über die generative und vegetative Vermehrung der Samen-pflanzen in der alpinen Vegetation Petsamo-Lappland. I, II, Annales Botanici Societatis Zoologicae-Botanicae Fennicae Vanamo 11: 1-323 and 14: 1-405.

Spencer, K. A. 1969. The Agromyzidae of Canada and Alaska. Memoirs of the Entomological Society of Canada. Number 64. The Entomological Society of Canada., Ottawa. 311 p.

Sprague, E. F. 1960. Ecological life history of California species of Pedicularis. Unpublished Ph.D. thesis, Claremont Graduate School, University Microfilms, Inc., Ann Arbor, Michigan. 193 p.

_____ 1962a. Parasitism in Pedicularis. Madrono 16: 192-200.

_____ 1962b. Pollination and evolution in Pedicularis (Scrophulariaceae). Aliso 5: 181-209.

Steel, R. G. D. and J. H. Torrie. 1960. Principles and procedures of statistics. McGraw-Hill Book Company, Inc., New York. 481 p.

Strid, A. 1969. Evolutionary trends in the breeding system of Nigella (Ranunculaceae). Botaniska Notiser 122: 380-397.

Tamm, C. O. 1948. Observations on reproduction and survival of some perennial herbs. Botaniska Notiser 3: 305-321.

_____ 1956. Further observations on the survival and flowering of some perennial herbs. I. Oikos 7: 273-292.

Tedrow, J. C. F. 1968. Pedogenic gradients of the polar regions. Journal of Soil Science 19: 197-204.

Thompson, H. A. 1965. The climate of the Canadian Arctic. Canada Department of Transport, Meteorological Branch, Toronto. 32 p.

_____ 1968. The climate of Hudson Bay, p. 263-286. In C. S. Beals (ed.), Science, history and Hudson Bay. Volume I. Queen's Printer, Ottawa.

Tsoong, P. C. and K. T. Chang. 1965. Palynological study of Pedicularis and its relation with the taxonomic systems of the genus. (In Chinese). Acta Phytotaxonomica Sinica 10: 257-281, 357-374.

van Steveninck, R. F. M. 1957. Factors affecting the abscission of reproductive organs in yellow lupins (Lupinus luteus L.) Part 1. The effect of different patterns of flower removal. Journal of Experimental Botany 8: 373-381.

Vockeroth, J. R. 1958. Distribution patterns of the Scatomyzinae (Diptera, Muscidae). Proceedings of the 10th International Congress of Entomology 1: 619-625.

Volkart, A. 1899. Untersuchungen über den Parasitismus der Pedicularisarten. Dissertation, University of Zürich, Zürich. 52 p.

Warming, E. 1908. Ericineae (Ericaceae, Pirolaceae). Morphology and biology. (Structure and biology of arctic flowering plants 1, 1). Medelelser om Grønland 36: 1-71.

Watts, L. E. 1968. Levels of compatibility in Brassica oleracea. Heredity 23: 119-125.

Weeden, R. B. 1968. Dates of first flowers of alpine plants at Eagle Creek, central Alaska. Canadian Field-Naturalist 82: 24-31.

Wettstein, R. von. 1891. Scrophulariaceae. In Engler and Prantl, Die naturlichen Pflanzenfamilien IV (3b): 39-107.

Wilkins, D. A. 1963. Plasticity and establishment in Euphrasia. Annals of Botany, New Series, 27(107): 533-552.

Williams, M. Y. 1948. The geological history of Churchill, Manitoba. Western Miner 21: 39-42.

Zhukova, P. G. 1966. Chromosome numbers in some species of plants of the northeastern part of the USSR. I. Botanicheskii Zhurnal 51: 1511-1516.